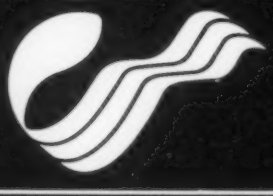

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Link Between Long-Term Variability in Upwelling and Fish Production in the Northeast Pacific Ocean

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The biomass of pelagic fish in the Coastal Upwelling Domain off the west coast of North America decreased by a factor of 5 in the first half of this century. We assemble several physical and biological time series spanning this period to determine what may have caused this decline in productivity. Based on an observed link between time series of the coastal wind and primary production, we conclude that there was a strong relaxation in wind-induced upwelling and primary production between 1916 and 1942 off southern California. The fact that the individual biomasses of the dominant pelagic fish species tend to rise and fall in phase through the sediment record off southern California is consistent with our belief that these species are responding to a long-period (40–60 yr) oscillation in primary and secondary production, which, in turn, is being forced by a long-period oscillation in wind-induced upwelling. Our extended sardine recruitment time series indicates that there is a nonlinear relationship between Pacific sardine (*Sardinops sagax*) recruitment and upwelling and suggests that optimal recruitment occurs when the wind speed during the first few months of life averages 7–8 m/s.

La biomasse de poisson pélagique dans le domaine côtier de remontée des eaux sur la côte ouest de l'Amérique du Nord a diminué d'un facteur 5 au cours de la première moitié du siècle. Nous avons réuni plusieurs séries chronologiques, physiques et biologiques, couvrant cette période pour déterminer les raisons possibles de cette baisse de productivité. Ayant observé un lien entre les séries chronologiques relatives au vent côtier et à la production primaire, nous en avons conclu qu'il y avait eu une forte relation entre la remontée des eaux due au vent et la production primnaire entre 1916 et 1942, au large de la Californie du sud. Le fait que les biomasses des différentes espaces, prises séparément, aient tendance à augmenter et à diminuer en phase, au large de la Californie du sud, si l'on en juge par les sédiments, confirme ce que nous pensions, c'est-à-dire que les espèces suivent des oscillations de longue période (40–60 ans), en ce qui concerne les productions primaire et secondaire, lesquelles seraient provoquées par des oscilations de longue période de la remontée des eaux due au vent. Nos séries chronologiques étendues sur le recrutement des sardines indiquent qu'il existe une relation non linéaire entre le recrutement des sardines et la remontée des eaux, le recrutement optimal correspondant à une vitesse du vent, pendant les premiers mois de la vie, de 7–8 m/s en moyenne.

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A recent review by Ware and McFarlane (1989) concluded that there are three major fisheries production domains (and a transitional zone) in the northeast Pacific Ocean (Fig. 1). The most southern one, the Coastal Upwelling Domain, extends from Baja California (25–28°N) to the northern tip of Vancouver Island (51°N). Within this region, upwelling occurs most of the year off California and from May through September off Vancouver Island. Smith's (1978) reanalysis of Soutar and Isaacs' (1974) landmark study of the paleoclimatology of the southern California Bight established that the Coastal Upwelling Domain has been dominated for the last two centuries by three species of pelagic fish: Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*), and Northern anchovy (*Engraulis mordax*). All of these species, except anchovy, undertake an extensive annual migration from spawning grounds off southern California, north to feeding grounds off Washington and southern British Columbia, a distance of 15–20° of latitude. The return leg of this journey is completed late in the fall.

Since the 1870s the pelagic fish biomass in the Coastal Upwelling Domain has averaged about 11 million tonnes (t) (Smith 1978): 8 million t of hake (Fig 2A), 3 million t of sardine (Fig. 2B), and 0.3–1 million t of anchovy. The combined biomass of these species was well above average at the turn of the century and declined sharply from approximately 25 million t in 1905 to 4.5 million t by 1950. The biomass continued to decline and since 1965 has become totally dominated by hake, whose biomass has fluctuated between 1 and 2.5 million t (Francis et al. 1984). Northern anchovy increased off southern California in the early 1970s reaching a peak of 2 million t in 1974, but the stock has recently declined to an average level of 0.7 million t (Methot 1989). The Pacific sardine stock, currently around 50 000 t, is well below its long-term average level of 3 million t. Smith and Moser (1988) observed that the bio-

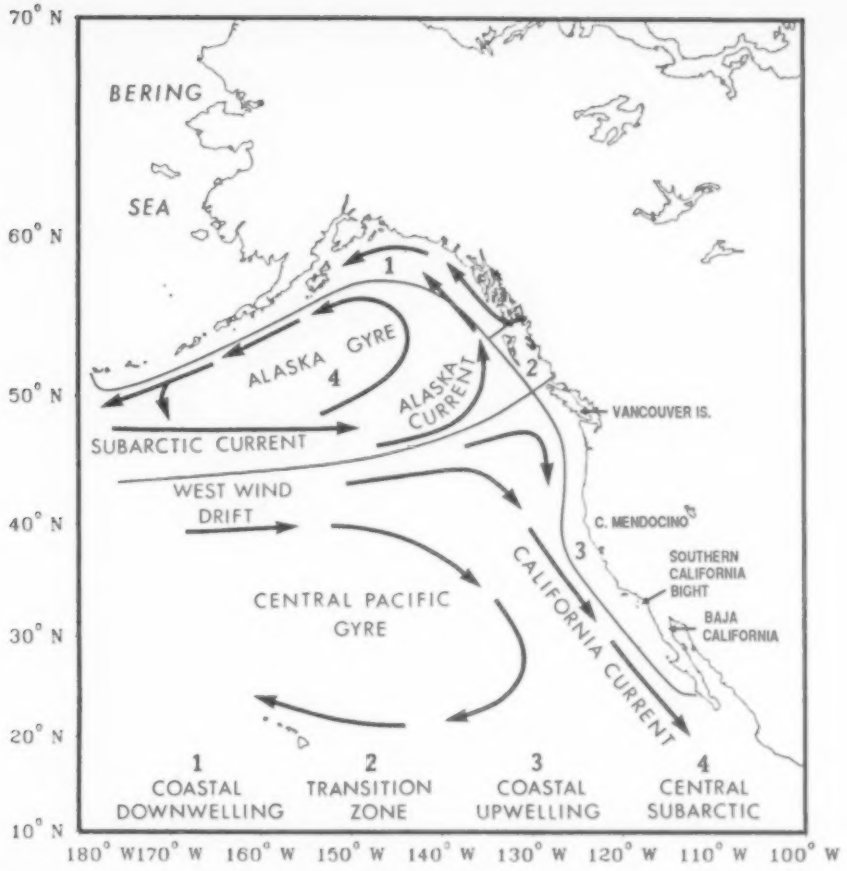

FIG. 1. Fisheries production domains and general circulation in the northeast Pacific Ocean (from Ware and McFarlane 1989). Some key place names mentioned in the text are shown.

mass of these three pelagic species has tended to rise and fall in phase over the last 200 yr (Fig. 2C), largely in response to environmental conditons, because fishing was not a major factor until the 1930s.

In a recent study, Cury and Roy (1989) examined time series of sardine recruitment in four stocks around the world. They found a nonlinear relationship between recruitment and upwelling intensity in places where upwelling was driven by strong, alongshore winds. In these stocks, maximum recruitment occurred at average annual wind speeds of 5–6 m/s. For the case of the California sardine, they concluded that the stock collapsed in the late 1950s because of excessive upwelling and a depressed parent stock caused by overfishing (MacCall 1979).

The objective of this paper is to review what we know about ocean climate in the northern and southern parts of the Coastal Upwelling Domain over the last 200 yr to determine if the Cury–Roy hypothesis can be extended to explain the fluctuations in sardine biomass during this period, and particularly during the first half of this century, as well as the concurrent changes in hake biomass (Fig. 2). Because anchovy has been a relatively minor member of the pelagic community during this period, we have limited our analysis to sardine and hake. We place more emphasis on sardine because more is known about this species.

Sardine and Hake Life Histories

Pacific Sardine

Growth and tagging studies indicate that there are two partially intermingling sardine stocks in the Coastal Upwelling Domain (Clark and Marr 1955). The northern stock ranges from southern California to British Columbia, while the southern stock occurs off Baja California.

The northern stock spawns primarily during the second quarter of the year (April, May, June) in the southern California Bight (MacCall and Prager 1988). The center of the spawning grounds is, on average, some 160 km offshore and roughly 100 km south of the center of the Bight (Kramer 1970). This spawning area is located southward (and downstream) of the region of highest winds, which occur off Cape Mendocino (Fig. 1). Husby and Nelson (1982) pointed out that sardines spawn in upwelling areas, but not in areas of intense upwelling. Historically, the main feeding and fishing concentrations of the northern stock were located 100–200 km downstream of the strong upwelling centers off Cape Mendicino and Pt. Conception (Clark and Marr 1955). Smith (1978) concluded that year-class strength in the northern sardine stock is established by environmental conditions off southern California.

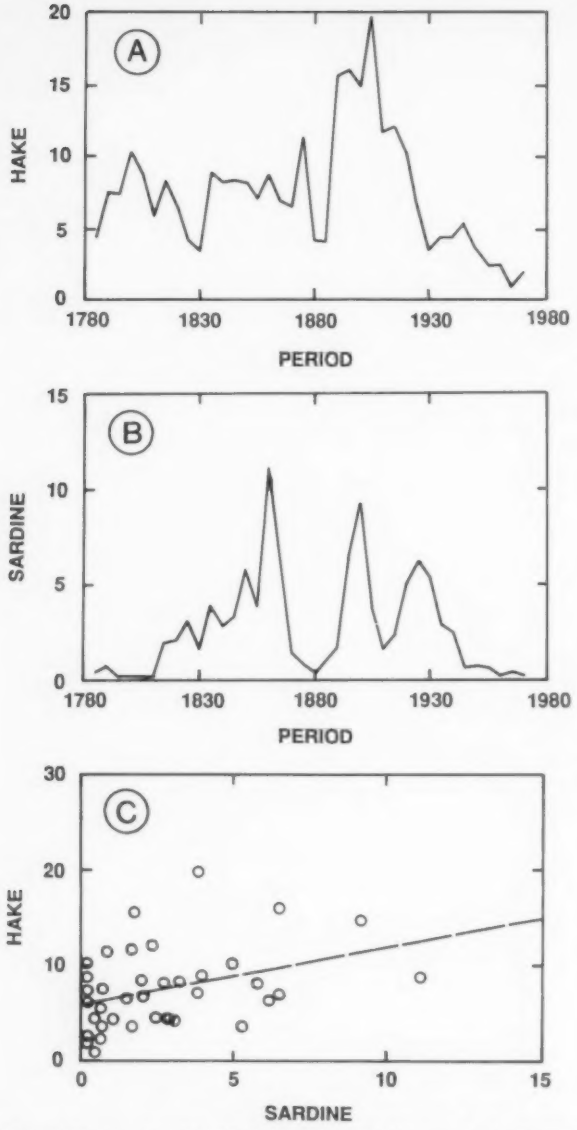

FIG. 2. Time series of Pacific hake and sardine biomass in the Coastal Upwelling Domain (in millions of tonnes) between 1785 and 1970. These estimates come from Smith (1978) who recalibrated Soutar and Isaacs' (1974) original data. Panel C shows that hake and sardine biomasses have tended to fluctuate in phase over the last 200 yr ($p = 0.02$).

The fact that sardine landings tended to be 50% lower in Washington and Oregon than in British Columbia suggests that after spawning, the northern sardine stock may have migrated largely seaward of the extensive body of cool, upwelled water typically found off Cape Mendicino and the Oregon coast. In the northern part of the Coastal Upwelling Domain off Vancouver Island, the considerably broader shelf, major nutrient input from Juan de Fuca Strait, and upwelling along the shelf-break and in the Juan de Fuca Eddy (Freeland and Denman 1982; Crawford and Dewey 1989) result in high primary and secondary production and an historically important sardine fishing area.

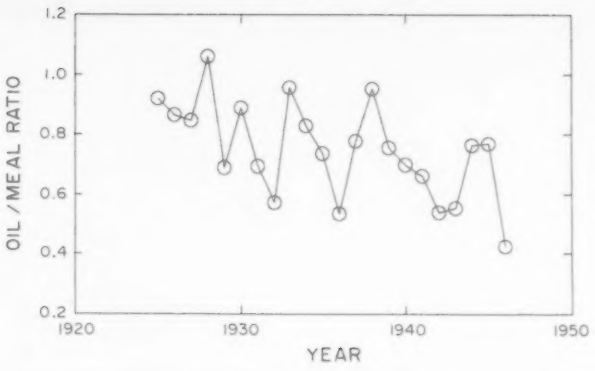

FIG. 3. Average sardine oil/meal ratio (fatness index) calculated from the annual yields obtained by the reduction plants along the west coast of Vancouver Island during the 22-yr history of the fishery (1925–46).

Pacific Hake

There is one large, migratory stock of hake in the Coastal Upwelling Domain. After spawning off southern California, adult hake migrate northward along the continental shelf and arrive on the feeding grounds off Washington and the west coast of Vancouver Island in late May – early June (Bailey et al. 1982). Feeding concentrations of hake remain in the Pacific Northwest until September–October, when they begin migrating back to the spawning grounds.

More than 90% of hake spawning occurs during the first quarter of the year (January, February, March) in the southern California Bight, but generally seaward of the sardine spawning grounds. After hatching, hake larvae feed on copepods. Bailey et al. (1982) believed that hake year-class strength is established sometime during the first year of life off southern California. Older, juvenile hake (ages 1–3 yr) are found primarily off southern and central California.

Data Sets

British Columbia Coast

A reduction fishery for sardine was prosecuted in southern British Columbia in the summer (July–October) from 1925 to 1945; it failed without warning in 1946 as the northern stock entered the final stage of its collapse. Annual statistics of the catch (tons) of Pacific sardine (called pilchard in British Columbia) and the resulting production of meal (tons) and oil (imperial gallons) along the west coast of Vancouver Island were obtained from an industry publication, *Western Fisheries* magazine. An imperial gallon of sardine oil weighs approximately 7.76 lb, so we were able to convert oil production to tons and calculate an annual oil/meal ratio (Fig. 3 and Appendix). This dimensionless index is a direct measure of body fatness: a high ratio implies a high fat content presumably resulting from favorable feeding conditions during the summer upwelling season.

Wind measurements for the first half of the century are not available for the British Columbia coast. As a consequence, we have used monthly mean observations of coastal salinities and

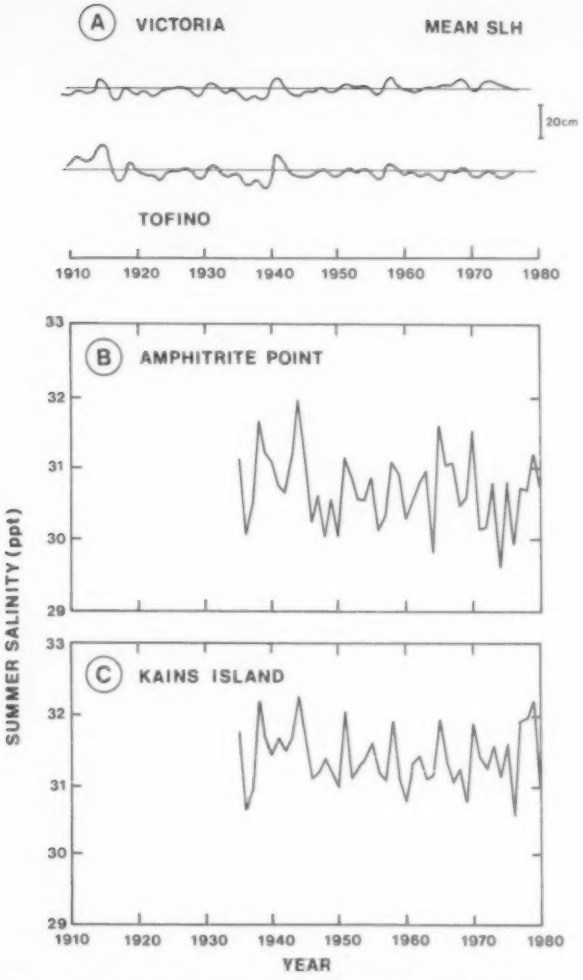

FIG. 4. Long-term monthly mean observations for the west coast of Vancouver Island: (A) low pass filtered sea level height (SLH) anomalies for Victoria (48.5°N, 123.4°W) and Tofino (49.1°N, 125.8°W) and summer (May–August) surface salinity at (B) Amphitrite Point (48.9°N, 125.5°W) and (C) Kains Island (50.4°N, 128.0°W).

sea levels to determine relative upwelling indicies at the northern end of the Coastal Upwelling Domain (Fig. 4). Sea level records dating from 1911 are available for Victoria (48.5°N) in Juan de Fuca Strait and from 1933 for Tofino (49.1°N) on the west coast of Vancouver Island (Fig. 1). Since these locations are connected by a broad strait, the monthly mean records show near identical variability. A transfer function based on 50 yr of overlap between the two time series has been used to extend the Tofino series back to 1911 (cf. Thomson and Tabata 1982). Salinity records for Amphitrite Point near Tofino (Fig. 40 and Kains Island (50.4°N) off northern Vancouver Island date back to 1935. Sea surface temperature records also are available for Victoria beginning in 1921 and closely track temperature records for the outer coast, which were first collected in the mid-1930s.

California Coast

Since sardine spawning peaks in May (MacCall and Prager 1988), northerly winds during the second quarter of the year (April–June) reflect upwelling conditions during the main spawning season. The averge northerly wind speed anomalies in the southern California Bight (30°N, 120°W) and off Cape Mendocino (40°N, 130°W) from 1899 to 1961 (Fig. 5) were compiled from Reid (1960) and from unpublished data files (I. Rodin, pers. comm.). Reid et al. (1958) and Husby and Nelson (1982) found that the average wind speed is lowest near the coast and increases seaward at a rate of about $0.02\ m \cdot s^{-1} \cdot km^{-1}$. The strongest winds typically occur about 200 km offshore. During the first 60 yr of this century the climatological northerly wind speed in the main spawning area of the sardine in April, May, and June has averaged 6.1 (±1.2), 7.0 (±1.1), and 7.3 (±0.9) m/s, respectively. The second quarter average speed is 6.8 m/s.

A time series of sardine year-class strength (which is a measure of the abundance of a cohort of fish in its year of birth) was created by merging Marr's (1960) time series with MacCall's (1979, his table 3) series. For Marr's series the relative abundance of sardine year-classes at Monterey and San Pedro were combined (Marr 1960, his table XIV). The correlation between the Marr and MacCall time series during the 11-yr period of overlap (1945–55) was used to generate an extended version of MacCall's series of absolute year-class abundance. Excluding Marr's underestimates of the strength of the 1948, 1949, and 1950 year-classes, the relationship between these two time series in year t is

$$R_{MC}(t) = 0.7 + 1/2\ R_M(t)$$

where R_{MC} and R_M are MacCall's and Marr's estimates (billions of fish), respectively ($r = 0.68$). MacCall's (1979, his fig. 7) assessment of the adult sardine biomass (tonnes) was used to calculate a recruit/parent stock time series between 1932 and 1960 (Fig. 6 and Appendix). This ratio is actually a measure of reproductive success and is preferable to the raw recruitment time series in our analysis because sardine recruitment after the 1930s could have been affected by overfishing of the parent stock (MacCall 1979). Thus the recruit/parent stock ratio tends to reflect the effect of environmental factors on recruitment because it adjusts for density-dependent changes in parent stock size.

Sardine and hake biomass estimates for the Coastal Upwelling Domain between 1785 and 1960 (Fig. 2) come from Smith (1978). (Anyone interested in anchovy should note that Smith's (1978) biomass estimates are too high by a factor of about 6–7 compared with Methot's (1989) reconstruction, which is considered to be the most accurate currently available. This correction reduces the importance of anchovy relative to sardine over the last 200 yr.)

For a measure of primary production, we found a time series of diatom abundance (Fig. 6 and Appendix) at Scripps pier between 1920 and 1943 (CalCOFI Prog. Rep. 1953). We have also used Smith and Eppley's (1982) primary production time series (1920–79) for the southern California Bight; this is a proxy series calculated from sea surface temperature and day-length information.

Results

Oceanic Conditions off British Columbia (1911–60)

The Victoria–Tofino tide gauge record (Fig. 4A) reveals a gradual fall in sea level between 1915 and 1940 followed by a rapid rise associated with the major 1940–41 El Niño – Southern

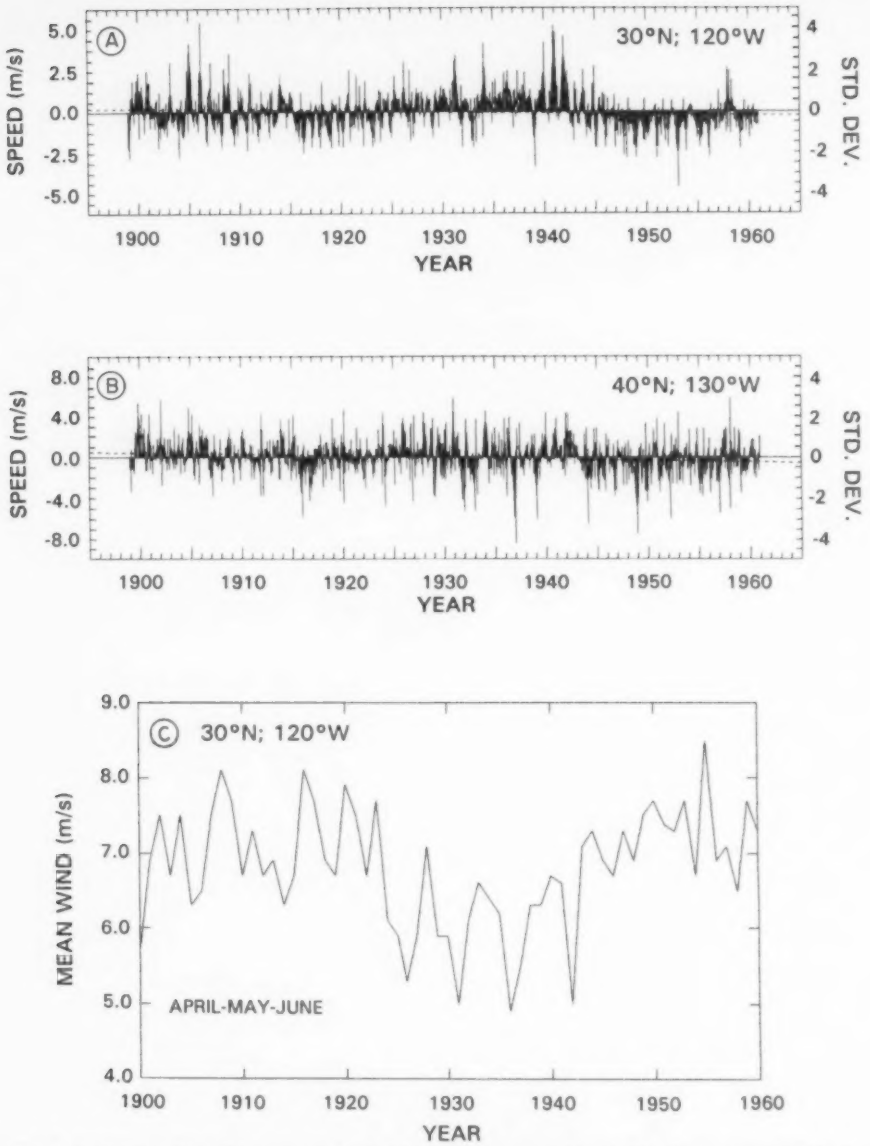

FIG. 5. Anomalies of monthly mean northerly (alongshore) geostrophic wind for the west coast of North America from 1899 to 1960. (A) 30°N, 120°W; (B) 40°N, 130°W; (C) average wind speed during the second quarter of the year (April–May–June) at 30°N, 120°W. Broken lines indicate trends.

Oscillation (ENSO) event (Quinn et al. 1978). Post-ENSO sea levels were higher than those in the late 1930s and gradually increased until the end of the next major ENSO event in 1957–58. The primary factors affecting the observed long-period variability in coastal sea levels are changes in steric height associated with variations in water density over the continental margin and changes in the direction and intensity of wind-forced regional currents. Because currents along the continental margin are in near geostrophic balance, intensified upwelling-favorable northerly winds will cause coastal sea level to fall, while intensified downwelling-favorable southerly winds cause sea level to rise. The decline in sea level during upwelling conditions is further compounded by increased densities (lower steric levels) over the continental shelf. Based on these arguments, the declining sea levels observed during the early part of the century were associated with intensifying northerly (or weakening southerly) upwelling-favorable winds. Following the greatly reduced upwelling conditions during the 1940–41 ENSO event, upwelling off the British Columbia coast remained comparatively weak until the late 1950s.

Concurrent with these changes in sea level, the average summer (May–August) salinity off the west coast of Vancouver Island rose in the late 1930s and then declined following the 1940–41 ENSO event (Fig. 4). The close in-phase relationship between upwelling-favorable winds off Cape Flattery (Bakun upwelling index, Bakun 1973) and Amphitrite Point salinity

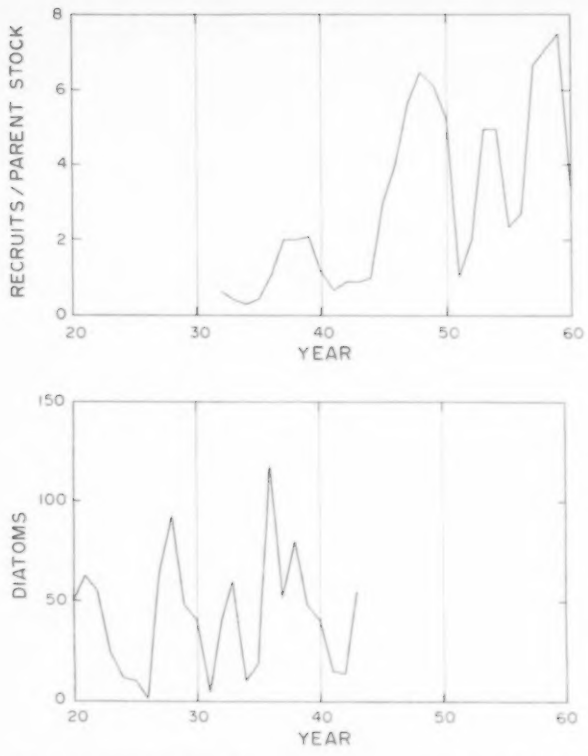

FIG. 6. Time series of sardine reproductive success (thousands of age 2 recruits per tonne of parent stock) and diatom abundance (thousands of cells per litre). Smith and Eppley's (1982) data suggest that the anomalously high diatom count at Scripps pier in 1936 may have been a local phenomenon that was not generally representative of conditions throughout the southern California Bight.

during the summer months suggests that coastal water properties off southern Vancouver Island are affected principally by three processes: (1) upwelling in the Juan de Fuca Eddy (Freeland and Denman 1982), (2) alongshore advection from the strong upwelling center off Cape Scott and Brooks Peninsula (Ware and Thomson 1989), and to a lesser extent (3) upwelling and cross-shelf mixing along the shelf-break. Coastal salinities in summer are also affected by runoff from Barkley Sound and freshwater discharge from the Fraser River, which reaches the outer coast via Juan de Fuca Strait and gives rise to the buoyancy-driven Vancouver Island Coastal Current over the inner Vancouver Island shelf (Thomson et al. 1989; Griffin and LeBlond 1990; Hickey et al. 1991). The poleward transport of relatively cold, low-salinity water by this current is impeded by northerly winds and augmented by southerly winds. Thus, increased salinities at Amphitrite Point and Kains Island are associated with upwelling-favorable winds and decreased salinities with downwelling-favorable winds, consistent with the results of the Tofino sea level record. The fact that the coastal salinity is positively correlated with the Bakun upwelling index over the length of these records (1946–85; $p = 0.0001$) supports our contention that salinity is positively linked to local upwelling-favorable winds, as well as to the attendant reduction in northward transport by the Vancouver Island Coastal Current.

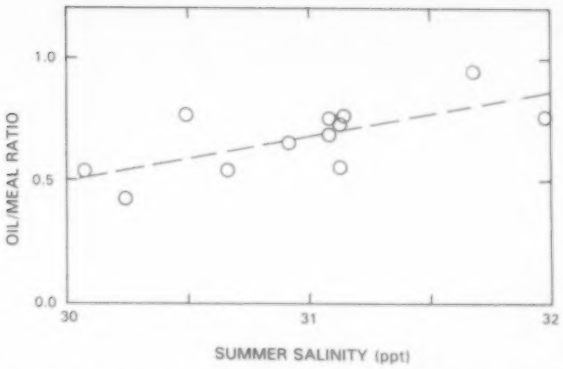

FIG. 7. Correlation between sardine fatness index and the summer (May–August) surface salinity at Amphitrite Point. Over the 12 yr of overlap, summer salinity explains 48% of the variance in sardine fatness, and summer sea level explains an additional 12%.

The observed fall in salinity in the mid-1940s may have been caused by increased runoff (Amphitrite Point salinity and Fraser River discharge are negatively correlated during this period, $p = 0.037$) and by a decrease in the intensity of upwelling-favorable winds. The possibility of reduced upwelling is supported by the fact that Kains Island salinity also fell during this period, even though Kains Island salinity and Fraser River discharge are not significantly correlated. Increased runoff, decreased upwelling, and increased transport by the coastal curent would all tend to lower salinity, and presumably nutrient levels, in the euphotic zone over the coastal fishing banks.

The sea surface warming that occurred off the British Columbia coast from 1915 to 1943 (Thomson et al. 1984) was part of a worldwide phenomenon observed in a wide variety of global time series of temperature and related proxy variables (Stocker and Mysak 1989). Air temperatures from England, the extent of mountain glaciers in Switzerland, and tree ring records from North America all indicate a particularly strong warming period during the first half of this century. Air temperatures from southern British Columbia were well below the climatological mean from 1900 to 1923 but generally above the mean from 1924 to 1947 (Dodimead 1984). The latter was the most protracted warm period in this region so far in this century (the current warm period is only into its 13th year; 1977–90).

Sardine Fatness Index (1925–46)

Sardines were fished commercially off the west coast of Vancouver Island from 1925 to 1946. Most of the annual catch, which averaged 40 000 t, was reduced to fish meal and oil. From reduction plant records of the catch and the resulting yields of meal and oil, we calculate that, on average, the sardine body composition consisted of 18% meal, 14% oil, and 68% water (by weight). The oil/total catch and oil/meal ratios (Fig. 3) are positively correlated and are direct measures of the degree of fatness (or physiological condition) during the summer fishing season (late June to mid-October).

For the duration of the British Columbia fishery there was a significant time-dependent decline in sardine fatness ($p = 0.006$; Fig. 3). The interannual variability in this index is highly correlated with concurrent variations in summer salinity during the 12-yr period that these time series overlap ($p = 0.01$; Fig. 7). In addition, sardine fatness and sea level are negatively

correlated ($p = 0.05$). Together, summer salinity and sea level explain 60% of the variance in the oil/meal ratio. From this we infer that a higher salinity (and lower sea level) reflects a higher nutrient load in the euphotic zone, which, in turn, enhances diatom and copepod production. Because these are the principal foods of sardines in British Columbia (Hart and Wailes 1932), the statistical data suggest that the decline in the sardine fatness index in the late 1930s and 1940s coincided with a relaxation of upwelling on the feeding grounds.

Oceanic Conditions off Southern California (1900–60)

Instrument-derived information on oceanic conditions off California is sketchy prior to the late 1940s. The sea level pressure data indicate that there was a striking decrease in the strength of upwelling-favorable coastal winds at 30°N between 1916 and 1942 (Fig. 5). Coincidentally, there was a general rise in average sea level at San Francisco and San Diego (Thomson and Tabata 1982) indicative of decreased upwelling-favorable winds, contrary to what occurred along the British Columbia coast. After the 1940–41 ENSO event the strength of the summer coastal winds increased for the next two decades, reaching a broad peak in the mid-1950s to early 1970s (Bakun 1973). Since then, the summer winds have fallen back toward their climatological mean state (Bakun 1990).

Plankton and Pelagic Fish Biomass of Southern California

Diatom abundance (measured at Scripps pier), second quarter wind speed, and sardine reproductive success exhibited large fluctuations between 1920 and 1943 (Fig. 5 and 6). Although the data are noisy (in part due to measurement error), there are significant linear correlations between these variables (Fig. 8). However, closer inspection of some of these relationships using either a lowess or distance weighted least squares smoother indicates that they may be nonlinear. For example, in Fig. 8A, the abundance of diatoms significantly increased ($p = 0.03$) with the average wind speed during the second quarter (April–June); however, there is a hint that diatom abundance may be maximized at wind speeds between 7 and 8 m/s. In contrast, sardine reproductive success is positively correlated ($p = 0.05$) with diatom abundance over the entire range of observation (Fig. 8B). In Fig. 8C, sardine reproductive success clearly increases with wind speed up to 8 m/s ($p = 0.01$); although there is only a single observation beyond this point, it suggests that sardine reproductive success may decline at higher wind speeds as Cury and Roy (1989) found.

Another significant piece of evidence linking biological production and fish reproductive success to the wind is that Smith and Epply's (1982) primary production estimates in the southern California Bight during the second quarter (Fig. 9) are positively correlated ($p = 0.003$) with the average wind speed for the same period. In fact, in the southern California Bight the strongest winds (Husby and Nelson 1982), highest primary production (Smith and Eppley 1982), and sardine peak spawning (MacCall and Prager 1988) all occur in the second quarter.

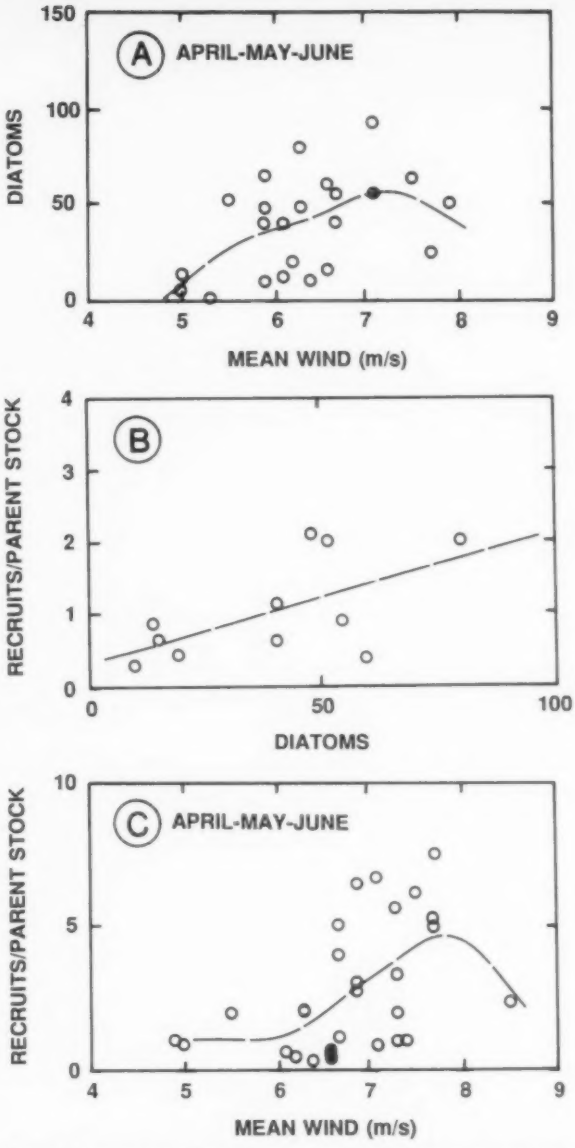

FIG. 8. Distance weighted least squares relationships between (A) diatom abundance and second quarter wind speed (linear correlation $p = 0.03$), (B) sardine recruits/parent stock and diatom abundance in the year of birth (linear correlation $p = 0.05$), and (c) sardine recruits/parent stock ratio and second quarter wind speed during the year of birth (linear correlation $p = 0.01$). In Fig. 8A and 8B the 1936 diatom count appeared to be an outlier and was excluded from these comparisons (see Fig. 6 caption).

Discussion

Double Jeopardy Hypothesis

Our analysis of the ocean climate and sardine biomass time series during the first half of this century suggests that the sardine's most recent demise was initiated by a strong relaxation in the strength of the northerly winds in the southern part of the Coastal Upwelling Domain (Fig. 5C). This, in turn, would have caused a coincident drop in primary production (Fig. 9) in the sardine's main spawning and nursery area. The sharp decline in sardine and hake biomass (Fig. 2) between 1916 and 1942 probably reflects this decrease in biological productivity.

Besides Reid's northerly wind time series, there is other evidence supporting a decline in upwelling off southern

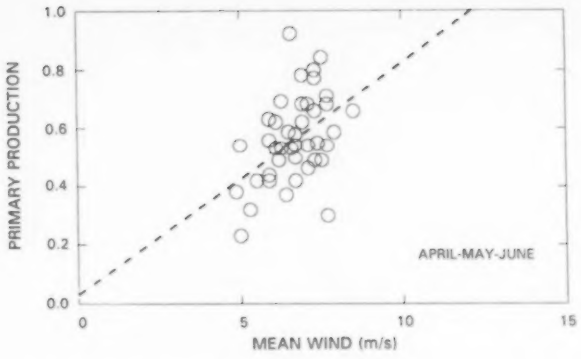

FIG. 9. Linear relationship between the second quarter wind speed and Smith and Eppleys' (1982) estimates of second quarter primary production (g $C \cdot m^{-2} \cdot d^{-1}$) in the southern California Bight ($p < 0.001$).

California between 1916 and 1942. Douglas' (1980) sea surface temperature time series, reconstructed from tree ring data, indicates that winter and spring temperatures off southern California cooled in the 1890s, reaching a minimum around 1905. Since wind speed and water temperature tend to be negatively correlated, Douglas' proxy time series for southern California suggest that the winds reached a maximum between 1900 and 1910 and then weakened for the next 30 yr. In this context, the tree ring data agree with Reid's wind time series (30°N; Fig. 5). Dunbar's (1983) stable oxygen isotope record also indicates that winter and spring sea temperatures in the southern California Bight were warm after 1920, which is consistent with a relaxation in upwelling (Fig. 10).

Given that the second quarter wind speed decreased from 7.2 to 5.9 m/s between 1916 and 1942, how much of a decline in primary production might be caused by a 1.3 m/s relaxation? The turbulence-transport diagram in Parrish et al. (1983, their fig. 7) suggests that a change of this magnitude would cause a six- to sevenfold reduction (from 0.9 to 0.13 $t \cdot s^{-1} \cdot m^{-1}$) in offshore Ekman transport in the southern California Bight. Using published data from various upwelling regions around the world, we find that primary production is roughly proportional to Ekman transport (D. M. Ware, in prep.). Consequently, a 1.3 m/s decrease in average wind speed in the southern California Bight could cause about a six- to sevenfold decrease in primary production. We suggest that this decline in wind speed and primary production is largely responsible for the more than fivefold decrease in pelagic fish biomass, from 25 million t in 1900 to 4.5 million t by 1950. The decline in the sardine stock during this period was also aggravated by the fact that it was becoming increasingly overfished after 1935 (MacCall 1979).

In the northern part of the Coastal Upwelling Domain, large-scale changes in coastal runoff and a decline in upwelling-favorable winds caused the summer salinity off the south coast of British Columbia to fall throughout the 1940s. The concurrent rise in coastal sea level confirms that this was associated with weakened alongshore winds (Fig. 10). Sardine fatness is positively linked to the trend in salinity during this period, implying that a lower salt content is associated with reduced nutrient levels, and consequently a lower production

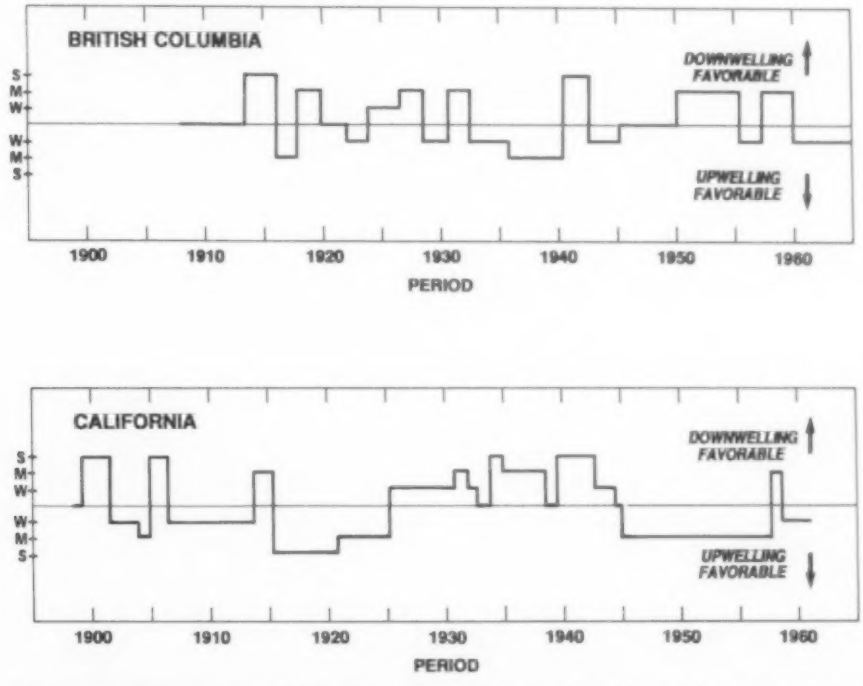

FIG. 10. Schematic time series of upwelling- versus downwelling-favorable conditions in the northern and southern portions of the Coastal Upwelling Domain. The British Columbia series is based on sea level and geostrophic wind data; the California series is based on geostrophic winds. S = strong; M = moderate; W = weak.

of diatoms and copepods that form the sardine's principal foods. This declining trend in the state of the summer food supply may have had some effect on the physiological condition of the adult sardine which fed off Washington and British Columbia.

The last and most critical link between sardine productivity and upwelling-favorable winds stems from the evidence that sardine reproductive success increases with diatom abundance (Fig. 8B). Presumably, this correlation reflects the fact that a higher abundance of diatoms in the southern California Bight is able to support more sardines, either directly as food or indirectly by increasing the numbers of small copepods, which are also important prey (CALCOFI Prog. Rep. 1953).

Thus, natural events in the first half of this century in both the northern and southern portions of the Coastal Upwelling Domain placed the sardines in a state of double jeopardy: (1) a declining trend in recruitment from the main spawning and rearing areas in the southern portion of the Coastal Upwelling Domain, due to a general worsening of feeding conditions from 1916 to 1942, and (2) a general deterioration of feeding conditions (and possibly physiological condition) of the component of the stock which fed off British Columbia between 1935 and 1946.

Test of the Cury–Roy Hypothesis

Cury and Roy (1989) found that sardine recruitment peaked at an *annual average* alongshore wind speed of 5–6 m/s off Monterey, California. Figure 8C spans a longer period (1932–60) and tests a different wind time series than Curry and Roy used. In general, it is consistent with the nonlinear relationship they discovered. Although the optimal wind speed is not well defined in our analysis, the highest sardine reproductive success occurred at wind speeds between 7 and 8 m/s (Fig. 8C).

Part of the reason Cury and Roy found a lower optimum is because they used an average, *annual* upwelling index whereas we reference sardine reproductive success to the wind speed during the peak spawning season (April–June). Characteristic monthly wind speeds in the strongest upwelling areas around the world average about 10 m/s (Parrish et al. 1983). These sites are locally unproductive because the recently upwelled nutrients have not had sufficient time to develop a phytoplankton community. Comparative studies of upwelling systems indicate that the largest standing stocks of zooplankton and pelagic fish tend to be downstream of these intense upwelling regions (Parrish et al. 1983). This implies that the optimal wind speed for sardine recruitment is less than 10 m/s. Since it is believed that sardine year-class strength is established by the early juvenile stage (P. Smith, pers. comm.), reproductive success is likely to be most sensitive to the strength of the winds during the first few months of life. Since the second quarter wind speed averages 6.8 m/s (at 30°N, 120°W), our findings suggest that sardine reproductive success in the southern California Bight is maximized at wind speeds about 1 m/s above the climatological mean.

Long-Term Changes in Production

There is some compelling evidence in the sediment record that biological productivity in the southern California Bight has been strongly linked to upwelling for the last 200 yr, at least. In a recent paper, Dunbar (1983) presented an oxygen isotope record of upwelling around the Santa Barbara basin dating back to 1750 (Fig. 11). Smith's (1978) reconstruction of the hake and sardine biomass in the same area date back to 1785

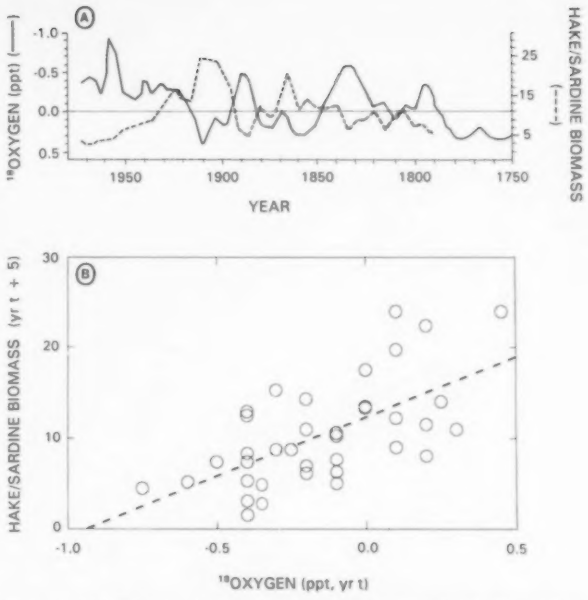

FIG. 11. (A) ^{18}Oxygen isotope variation in the upwelling-indicator foraminifer *Globigerina bulloides* (solid line; Dunbar 1983), and the combined sardine and hake biomass between 1785 and 1970 (broken line; Smith 1978) and (B) correlation between these two time series when the isotope record leads the fish biomass record by 5 yr ($p < 0.0001$).

(Fig. 11). A cross-correlation analysis of these time series indicates that the combined hake and sardine biomass, the hake biomass, and the sardine biomass were all positively (and significantly) correlated with Dunbar's oxygen isotope ratio. In all three cases, the maximum correlation occurred with a 5-yr lag (maximum isotope ratio leads maximum fish biomass by 5 yr; Fig. 11). A positive isotope ratio signifies a cool winter and spring due to increased upwelling); hence the cross-correlation function indicates that the pelagic fish biomass peaks about 5 yr after a rise in upwelling and biological productivity. According to the oxygen isotope time series, upwelling was particularly intense around 1810, 1860, and 1910 (Fig. 11). This roughly 50-yr periodicity appears clearly in the oxygen isotope autocorrelation function. Douglas' (1980) sea surface temperature reconstruction from proxy data also indicates a 50-yr oscillation in summer temperatures off California. An oscillation of this period is consistent with Reid's (1960) wind time series and subsequent supplementary data (Bakun 1973; Mason and Bakun 1986), indicating that upwelling-favorable winds peaked between 1908 and 1915 in the southern California Bight, declined, and then rose to a second broad peak between 1955 and 1972, a roughly 50-yr cycle. Interestingly, this long-period oscillation in the winds is almost 180° out of phase with the general change in Northern Hemisphere nighttime marine air temperature, which shows a highly significant 60-yr periodicity (Kane and Teixeira 1990). The concurrence between these two time series suggests that changes in wind strength and the resulting mixing, upwelling, and temperature of the surface layer may be taking place over very large spatial scales.

We have presented evidence showing that the most recent relaxation in upwelling in the southern California Bight can explain the decline in pelagic fish biomass between 1910 and

1942; this hypothesis, however, does not explain why hake and sardine failed to recover when the northerly winds increased in the mid-1940s. As expected, sardine reproductive success improved significantly during this period, as evidenced by the high recruit/parent stock ratios (Fig. 6); however, by then the stock had been fished down to such a low level that it was unable to rebuild significantly. Later in the 1950s, upwelling-favorable winds may have been too intense as Cury and Roy (1989) suggested, although the importance of this factor is not as clear in the time series we examined (Fig. 8C). Perhaps the most significant observation is Dunbar's (1983) remark that the low isotope "values of *G. bulloides* in post-1930 deposits from the southern California Bight indicate warmer surface water, greater stratification of the water column, and less intense upwelling." If the surface layer was more stratified, then increased upwelling-favorable northerly winds in the 1950s and 1960s (Fig. 10) may have been unable to bring significantly more nutrient-rich water to the surface. Consequently, the decline in the sardine stock in this century was probably initiated by a sharp relaxation in upwelling in the 1920s, while its recovery was impaired by an intensive fishery in the 1950s, and possibly weak upwelling. The hake stock staged a modest recovery in the late 1940s (Smith 1978), but then faltered in the 1950s and became trapped in a fairly narrow range between 1 and 2 million t after 1960, possibly in response to the initiation of a fishery. For the reasons Dunbar (1983) mentioned, hake may have not recovered because the southern California Bight has not been particularly productive since 1920. The generally moderate levels of primary production (approximately 147 g $C \cdot m^{-2} \cdot yr^{-1}$) measured there in the 1970s (Smith and Eppley 1982) and the high post-1930s oxygen isotope ratio in the upwelling-indicator species Dunbar (1983) examined support this reduced productivity hypothesis.

In summary, we have built a circumstantial case that the biomass of sardines and hake in the Coastal Upwelling Domain reflects the general level of primary production, which in turn is linked to the intensity of upwelling-favorable winds off California. In addition, upwelling conditions off British Columbia, which can be out of phase with those off California (Fig. 10), may effect the physiological condition of the migratory fish stocks. We are not implying a simple one-to-one relationship where all pelagic species respond synchronously to a change in primary and secondary production. Obviously the system is not that simple; nevertheless, it merits repeating that the respective biomasses of sardine and hake in the southern California Bight have tended to rise and fall in phase, with a dominant 40- to 60-yr periodicity throughout the sediment record (Smith and Moser 1988). This general coupling is consistent with the conclusion that the pelagic fish stocks in the southern California Bight are responding to a long-period oscillation in primary and secondary production which, in turn, is being forced by a long-period oscillation in the coastal wind. This natural oscillation in the wind may be the primary source of the 40- to 60-yr periodicity in tree ring growth, oxygen isotope, and fish scale time series over the last 200 yr.

In addition to this broad relationship, other factors such as increased stratification are required to explain why the rise in upwelling-favorable winds after 1943 failed to stimulate primary and fish production. The reason why the productivity did not respond to wind-forcing is an unresolved question of considerable importance because what happens on the hake and sardine spawning and nursery grounds in the southern California Bight eventually impacts on the fisheries from California to British Columbia.

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Appendix

Table A.1. Time series of sardine year-class strength (billions of age 2 recruits), parent stock biomass (millions of tonnes), diatom abundance (thousands of cells per litre), British Columbia sardine oil/meal (fatness) ratio (dimensionless), and second quarter April–May–June (AMJ)) wind speed (m/s) at 30°N, 120°W.

Year	Recruits	Stock	Diatoms	Fatness ratio	AMJ wind
1920			50		7.9
1921			63		7.5
1922			55		6.7
1923			24		7.7
1924			12		6.1
1925			10	0.92	5.9
1926			1	0.86	5.3
1927	3.3		65	0.85	5.9
1928	2.5		93	1.06	7.1
1929	1.5		48	0.69	5.9
1930	1.1		40	0.88	5.9
1931	1.6		5	0.69	5.0
1932	2.1	3.3	40	0.57	6.1
1933	1.3	3.3	60	0.96	6.6
1934	1.0	3.4	10	0.82	6.4
1935	1.1	2.6	19	0.73	6.2
1936	2.0	1.9	118	0.54	4.9
1937	2.4	1.2	52	0.77	5.5
1938	2.4	1.2	80	0.95	6.3
1939	3.0	1.4	48	0.75	6.3
1940	1.9	1.7	40	0.70	6.7
1941	1.6	2.5	15	0.66	6.6
1942	1.8	2.1	14	0.54	5.0
1943	1.4	1.6	55	0.55	7.1
1944	1.2	1.2		0.76	7.3
1945	2.4	0.72		0.77	6.9
1946	1.6	0.57		0.42	6.7
1947	1.7	0.41			7.3
1948	3.9	0.74			6.9
1949	4.3	0.79			7.5
1950	3.7	0.78			7.7
1951	0.3	0.28			7.4
1952	0.4	0.14			7.3
1953	1.0	0.20			7.7
1954	1.2	0.24			6.7
1955	0.4	0.17			8.5
1956	0.3	0.11			6.9
1957	0.6	0.09			7.1
1958	1.6	0.18			6.5
1959	0.9	0.12			7.7
1960	0.3	0.09			7.3

Habitat Switch and Niche Overlap in Coregonid Fishes: Effects of Zooplankton Abundance

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Vendace (*Coregonus albula*) in Lake Mjøsa lived in the pelagic zone and gillnet catches were correlated with water temperature ($r^2 = 0.457$, $p < 0.005$). Whitefish (*Coregonus lavaretus*) exploited both epibenthic and pelagic areas. Whitefish with body lengths between 25 and 35 cm moved from the epibenthic to pelagic zone during summer; other length groups remained in epibenthic habitats. The pelagic fish returned to epibenthic areas in the autumn. Cladocerans were important food items for both fish species in the pelagic zone. The large copepod *Limnocalanus macrurus* was eaten only by vendace whereas surface insects were more important prey for whitefish. This suggests that vendace is the more specialized zooplanktivore. The pelagic gillnet catch of whitefish and the pelagic habitat overlap between whitefish and vendace increased with increasing zooplankton densities at depths between 0 and 50 m ($r^2 = 0.609$ and 0.494, respectively, $p<0.01$). During spring and autumn we observed a time lag between the change in zooplankton abundance and habitat switches of whitefish. The fish moved to the more profitable habitat several days after food availability had changed, indicating an element of learning in choice of habitat.

Le corégone blanc (*Coregonus albula*) du lac Mjøsa vivait dans la zone pélagique et les prises au filet maillant ont été corrélées avec la température de l'eau ($r^2 = 0{,}457$, $p < 0{,}005$). Le lavaret du Bourget (*Coregonus lavaretus*) a exploité les zones épibenthiques et pélagique. Les lavarets de 25 à 35 cm de long se déplaçaient de la zone épibenthique à la zone pélagique en été; les groupes de longueur différente demeuraient dans des habitats épibenthiques. Ce poisson pélagique retournait dans des zones épibenthiques à l'automne. Les deux espèces de poisson se nourrissaient surtout de cladocères dans la zone pélagique. Le grand copépode *Limnocalanus macrurus* n'était mangé que par le corégone blanc, tandis que les insectes de surface étaient des proies plus importantes pour le lavaret. Cela indique que le corégone blanc est le zooplanctivore plus spécialisé. Les prises de lavaret pélagique du corégone blanc et du lavaret ont augmenté avec la concentration croissante de zooplancton à des profondeurs de 0 à 50 m ($r^2 = 0{,}609$ et 0,494 respectivement, $p < 0{,}01$). Pendant l'été et à l'automne, nous avons observé un décalage de temps entre les variations d'abondance du zooplancton et les changements d'habitat du lavaret. Le poisson s'est déplacé dans l'habitat le plus propice plusieurs jours après que la nourriture vint à manquer, dénotant un élément d'apprentissage dans le choix d'habitat.

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Seasonal habitat switches of animals are supposed to result from changes in the environmental conditions, and habitat choices are considered to be trade-offs between profitabilities and risks in the environment (Stephens and Krebs 1986). Solitary animals will move from one food patch to another in order to maximize their energy gains (Charnov 1976), and animals may evaluate profits and costs of different habitats (Dill 1987; Werner and Hall 1988). Behaviour of fish may be modified by the process of learning about the quality of food patches (Milinski 1984; Werner and Hall 1988), by the risk of predation (Werner et al. 1983; Mittelbach 1984; Holbrook and Schmitt 1988), and by the presence of competitors (Pitcher et al. 1982).

In northern temperate lakes, prey abundance fluctuates seasonally and is an important factor influencing temporal habitat switches of fish. In many lakes, whitefish (*Coregonus lavaretus*) may exhibit seasonal habitat switches between benthic and pelagic habitats (Svärdson 1976). The closely related vendace (*Coregonus albula*) is usually pelagic when cooccurring with whitefish (Svärdson 1976; Nilsson 1979). In such situations the two fish species segregate in food selection (Hamrin and Persson 1986). Vendace is the more specialized zooplankton feeder whereas whitefish is a more generalized feeder, exploiting both epibenthic and pelagic food resources (Svärdson 1976; Hamrin and Persson 1986). Little is known, however, about the seasonal and spatial habitat use of these fishes in relation to pelagic food abundance.

Thus we studied habitat use of vendace and whitefish in Norwegian Lake Mjøsa where we tested (1) if habitat shifts of whitefish between epibenthic and pelagic habitats were correlated with the abundance of crustacean zooplankton, (2) if habitat overlaps between whitefish and vendace were correlated with the abundance of crustacean zooplankton, and (3) if diet overlaps between whitefish and vendace were correlated with the abundance of crustacean zooplankton.

TABLE 1. Mean annual CPUE of the most important fish species in Lake Mjøsa, 1978–80 (after Sandlund et al. 1985).

Species	Pelagic nets	Benthic nets
Brown trout (*Salmo trutta*)	0.1	<<0.1
Vendace (*Coregonus albula*)	0.9	0.1
Whitefish (*Coregonus lavaretus*)	0.4	1.4
Smelt (*Osmerus eperlanus*)	2.4	5.1
Roach (*Rutilus rutilus*)	<<0.1	3.4
Perch (*Perca fluviatilis*)	<<0.1	2.1
Ruffe (*Acerina cernua*)	<<0.1	4.3
Northern pike (*Esox lucius*)	<<0.1	<<0.1
Burbot (*Lota lota*)	0.0	0.9

Methods

Study Site

Mjøsa (61°30′N, 10°25′E) is a 449-m-deep oligo-mesotrophic, dimictic fjord lake and has a surface area of 365 km^2. The circulation periods last from late April until the end of June and from October until ice cover, usually in January–February (Holtan 1979). The thermocline is established at 12–20 m depth. In 1979, hypolimnetic temperatures varied between 3.5 and 8°C. Epilimnic temperatures reached 10°C by the middle of June and a maximum of 14°C in July. Total pelagic primary production in 1979 was approximately 20 g $C \cdot m^{-2} \cdot yr^{-1}$ (Kjellberg and Sandlund 1983).

A total of 20 crustacean zooplankton species occur in the pelagic zone in Mjøsa; 8 are copepods and 12 are cladocerans (Holtan et al. 1980). The most common are the copepods *Limnocalanus macrurus* Sars, *Eudiaptomus gracilis* Sars and *Cyclops lacustris* Sars and the cladocerans *Daphnia galeata* Sars, *D. cristata* Sars, and *Bosmina longispina* Leydig (Sandlund et al. 1991a).

Zoobenthos is dominated by chironomid larvae, oligochaetes, bivalves, and the amphipods *Pallasea quadrispinosa* Sars and *Gammaracanthus loricatus* Sabine (Holtan et al. 1980). *Mysis relicta* Lovén occurs in both epibenthic and pelagic habitats (Kjellberg and Sandlund 1983). Among zoobenthos eaten by epibenthic whitefish, chironomid larvae and pupae and *P. quadrispinosa* are the most important.

Mjøsa supports 20 fish species, with vendace, whitefish, and smelt (*Osmerus eperlanus*) being numerically dominant in the pelagic zone (Sandlund et al. 1985) (Table 1). In shallow water, roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), and ruffe (*Acerina cernua*) are the most numerous. The main predators are brown trout (*Salmo trutta*), burbot (*Lota lota*), and northern pike (*Esox lucius*).

Vendace and whitefish grow at about the same rate during the first 2 yr of life, reaching 11–12 cm at age 1 and 18–20 cm at age 2. The growth rate of vendace levels off earlier than for whitefish; asymptotic lengths and Brody's coefficient of the von Bertalanffy growth equations were respectively 22.7 cm and 1.03 for vendace and 31.0 cm and 0.52 for whitefish. The growth rate of males and females did not differ significantly ($p > 0.05$) (Næsje et al. 1986; Sandlund et al. 1991a).

Sampling

Zooplankton (February–December 1979), benthic insects and molluscs (May–November 1979), and fish (October 1978 – February 1980) were sampled at two localities in Mjøsa: Brøttum and Furnes. In both areas, maximum depth is around 90 m.

Zooplankton were sampled with a 25-L Schindler trap at the following depths: 0.5, 2, 5, 8, 10, 12, 16, 20, 30, and 50 m. One sample was taken at each depth (Langeland and Rognerud 1974) and subsequently identified and counted in an inverted microscope.

Benthic invertebrates were sampled with an Ekman grab (0.025 m^2, 0.5-mm bar mesh in screen) at the following depths: 0.5, 2, 4, 6, 8, 12, 20, and 50 m. The 0.5- and 2-m samples were omitted due to a stony substratum causing the Ekman grab to malfunction. Three replicate samples were taken at each depth in both sampling areas. Zoobenthos abundance was calculated as mean number and wet weight (grams) of animals per square metre, adjusted for the relative area of the sampled depth zones.

Fish were sampled by using epibenthic and pelagic gill nets. The gill nets consisted of 12 panels (panel size: epibenthic 25 × 2 m; pelagic 25 × 6 m) with varying mesh sizes (8- to 52-mm bar mesh, mesh increments 2 – 7 mm. Fish were sampled one to five 24-h periods at two pelagic and four epibenthic stations each month (except for December when only pelagic nets were used and January and March when sampling was omitted). The pelagic nets were placed at the following depths: 0–10, 10–30, 30–50, and 50–80 m. The epibenthic nets were set from the shoreline down to the deepest part of the sampling area (90 m). The exact depth of each net was registered with an echo sounder (Simrad EL). Catch per unit effort (CPUE) was calculated as number of fish per 100 m^2 of net area for 24 h of fishing.

Laboratory and Data Analyses

Fish were measured to the nearest 0.1 cm (natural tip length, Ricker 1979) and aged by burning and breaking the otoliths (Christensen 1964).

Stomach contents were analyzed and prey categories identified and counted under a stereoscopic microscope. Wet weight of stomach contents was estimated from undigested food items. The degree of diet overlap was calculated according to Schoener's (1968) similarity index $D = 1 - 1/2 \sum_{i=1}^{n} |p_i - q_i|$ where p_i is the weight proportion of food item i in population 1, q_i is the weight proportion of food item i in population 2, and n is the number of food categories. Index D varies between 0 and 1, representing no and complete food overlap, respectively. Degree of habitat overlap in the pelagic zone was calculated using Schoener's (1968) index, letting p_i and q_i represent the percentage of vendace and whitefish at the ith depth zone relative to the respective depth distributions of the species.

Zooplankton selection was estimated according to Ivlev's (1961) electivity index $E = (a - b)/(a + b)$ where a is the frequency by number of the prey organism in the stomach and b is the frequency by number of the prey organism in the environment.

Results

Zooplankton

The zooplankton community was dominated by *L. macrurus* (spring) and *E. gracilis*, *B. longispina*, *D. galeata*, and *D. cristata* (summer and early autumn) (Fig. 1). Densities of zooplankton were generally higher at Furnes than at Brøttum. At Furnes, maximum biomass of crustacean zooplankton occurred in August (6400 $mg \cdot m^{-2}$) and at Brøttum in July (2400 $mg \cdot m^{-2}$). At Furnes, maximum densities of adult *D. galeata* were recorded in August (7780 $ind. \cdot m^{-3}$) and

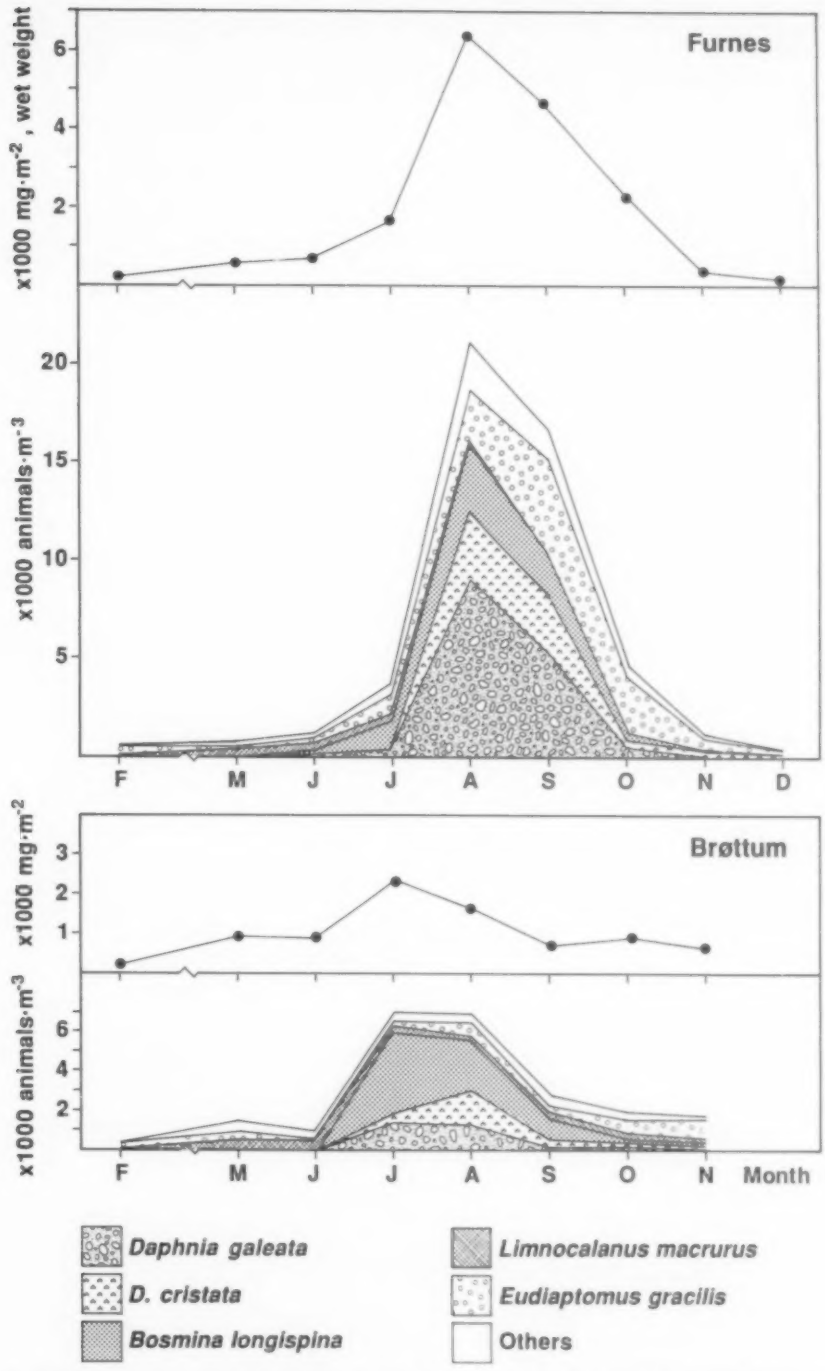

FIG. 1. Number of crustacean zooplankton in the 0–50 m depth zone in the sampling areas Furnes and Brøttum in Mjøsa, February–December 1979. Copepod nauplii and cladoceran embryos were omitted.

September (5100 ind.·m^{-3}). At Brøttum, densities of *D. galeata* were lower, with largest numbers of adults in July (1040 ind.·m^{-3}) and August (940 ind.·m^{-3}). At Furnes, *B. longispina* occurred in maximum densities in July (1320 ind.·m^{-3}), August (2880 ind.·m^{-3}), and September (1360 ind.·m^{-3}). Densities of *B. longispina* at Brøttum were higher, with maximum numbers in July (3220 ind.·m^{-3}), August (2240 ind.·m^{-3}), and September (1010 ind.·m^{-3}).

TABLE 2. Abundance (N, no.·m^{-2}) and wet weight (w, g·m^{-2}) (mean and standard deviation) of benthic insects and molluscs in the sampling areas Furnes and Brøttum in Mjøsa, 1979.

	Furnes				Brøttum			
Month	N	SD	w	SD	N	SD	w	SD
May	407.9	8.7	0.36	0.05	471.9	27.2	0.87	0.55
July	530.1	143.3	1.78	0.82	353.9	141.6	0.32	0.15
August	250.5	34.9	0.46	0.16	243.8	28.0	0.25	0.03
October	254.9	124.4	0.43	0.22	304.7	117.8	0.59	0.30
November	457.5	121.4	0.78	0.19	239.6	78.0	0.34	0.12

Zoobenthos

The zoobenthos in Mjøsa, as shown by Ekman grab samples, was dominated by chironomid larvae on most sampling dates (Holtan et al. 1980). Oligochaetes, the mollucs *Pisidium*, and the amphipode *P. quadrispinosa* were also common. Being a very mobile animal, *P. quadrispinosa* is able to avoid most zoobenthos samplers, and it was not sampled representatively with an Ekman grab.

The zoobenthos abundance in terms of wet weight and number of animals was highest in shallow waters (<10 m depth). The abundance and biomass of insects and molluscs, which were the zoobenthos groups eaten by whitefish, reached a maximum in July at Furnes and in May at Brøttum (Table 2).

Vendace and Whitefish

Habitat

A total of 1172 vendace and 1161 whitefish were caught. Very few whitefish and vendace were caught deeper than 50 m in the pelagic zone. Gill net catches of vendace were low in winter, spring, and early summer (November – July) (Fig. 2A). In epibenthic habitat CPUE of vendace remained low through the rest of the year, except for a slight increase in October at Brøttum, situated near the spawning grounds. CPUEs in the pelagic habitat, however, were high in late summer and autumn (August – October) (Fig. 2A). In June – July, pelagic vendace were mainly caught at depths between 0 and 10 m, but from August through November they were also abundant at depths between 10 and 30 m.

Whitefish were caught in both benthic and pelagic habitats (Fig. 2B). In the epibenthic habitat, mean CPUE of whitefish varied between 0.80 and 1.54. The pelagic catches of whitefish were very low during winter, spring, and early summer but increased during late summer and autumn. In both sampling areas, Brøttum and Furnes, a part of the whitefish population started to move into the pelagic habitat in July whereas maximum pelagic catches were taken in September (Fig. 2B). In November, most of the whitefish had returned to the epibenthic habitat. Pelagic densities of whitefish were highest at depths between 0 and 30 m.

Diet

In the pelagic zone, the diet of vendace and whitefish differed between the sampling areas (Fig. 3). At Furnes, vendace fed largely on the zooplankton species *B. longispina*, *D. galeata*, and *L. macrurus*. At Brøttum, vendace fed on the same food items, but the relative proportions were different. *Daphnia galeata* was less important whereas *L. macrurus* was more important as a food source (Mann–Whitney tests, $p < 0.05$). In addition, vendace at Brøttum also fed on *Leptodora kindti* (Focke) and fish (age 0 smelt).

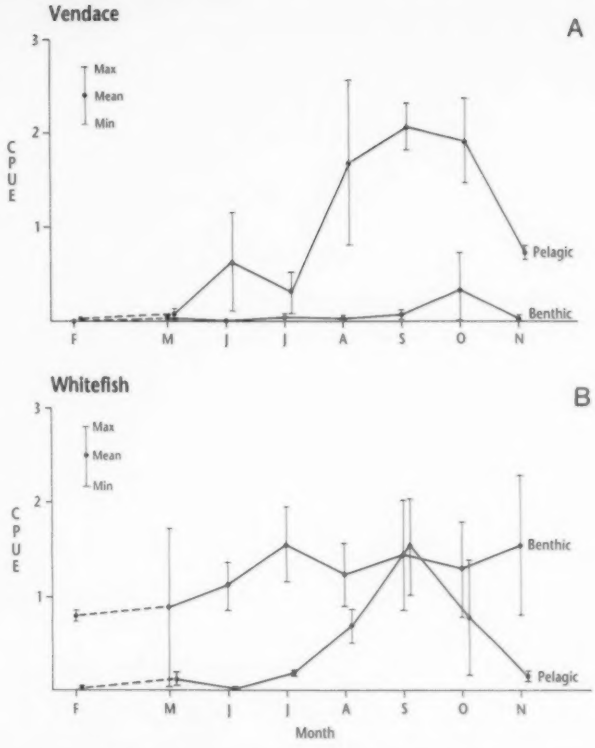

FIG. 2. CPUE of (A) vendace and (B) whitefish in pelagic and benthic gill nets, February–November 1979.

Whitefish fed largely on zooplankton in the pelagic zone (Fig. 3). At Furnes the most important zooplankters eaten were *L. kindti* and *D. galeata*. In addition, they fed on surface arthropods and fish (age 0 smelt). At Brøttum, whitefish fed on the same food items, but in addition, cyclopoid copepods were a more important food source. Whitefish caught in the pelagic zone appeared to stay in that zone for some time, as the frequency of bottom animals in their stomachs was very low. A small fraction of the amphipod *P. quadrispinosa*, however, indicated some exchange of fish between epibenthic and pelagic areas.

Based on estimates of Ivlev's (1961) electivity indices, vendace and whitefish appeared to differ in their selection of *L. macrurus* (Fig. 4). This species was positively selected by vendace during spring and late summer and autumn but was never selected by whitefish. Both vendace and whitefish selected *B. longispina* and *D. galeata* during summer and autumn, respectively. The large cladocerans *L. kindti* and *Bythotrephes longimanus* Leydig were also positively selected for shorter periods during summer. All other zooplankters were negatively selected.

Correlations in habitat and diet

The pelagic catches (CPUE) of vendace were more highly correlated with epilimnic water temperature (0–16 m) than with abundance of pelagic food, expressed as total number of crustacean zooplankton in 0–50 m depth (temperature: $r^2 = 0.457$, $p = 0.004$; zooplankton no.: $r^2 = 0.337$, $p = 0.018$) (Fig. 5A). On the other hand, the pelagic catches (CPUE) of whitefish showed higher correlation with number of crustacean

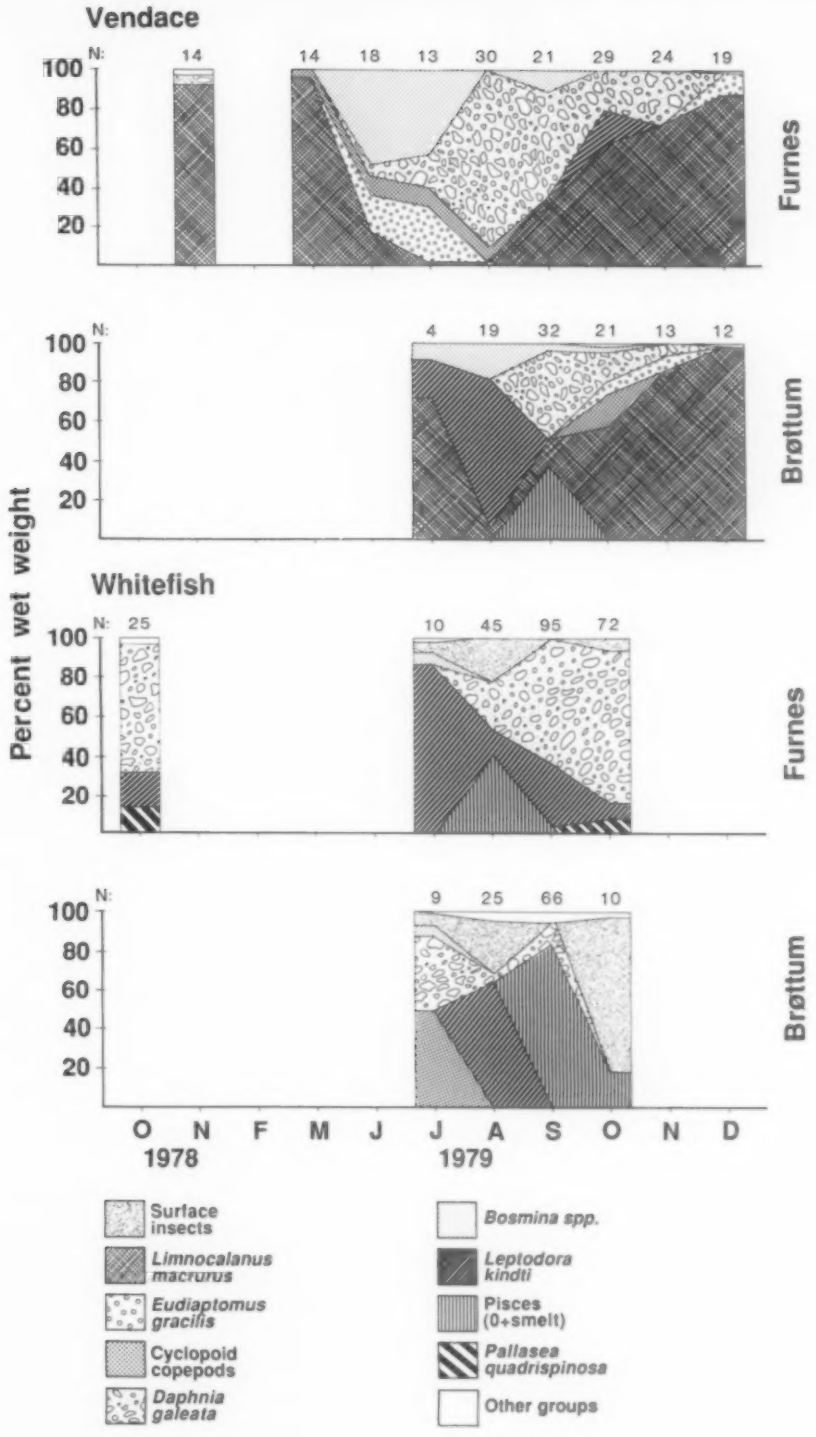

FIG. 3. Composition of stomach contents of pelagic vendace and whitefish in the sampling areas Furnes and Brøttum in Mjøsa, 1979.

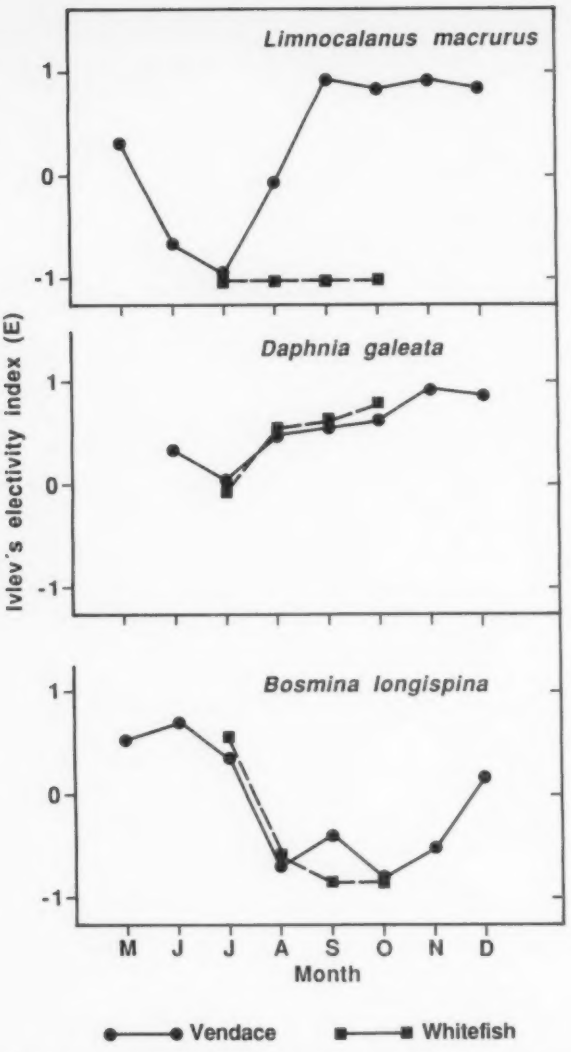

FIG. 4. Ivlev's electivity index (E) for the selection of three crustacean zooplankton species by pelagic whitefish (squares) and vendace (circles) at Furnes, May–December 1979.

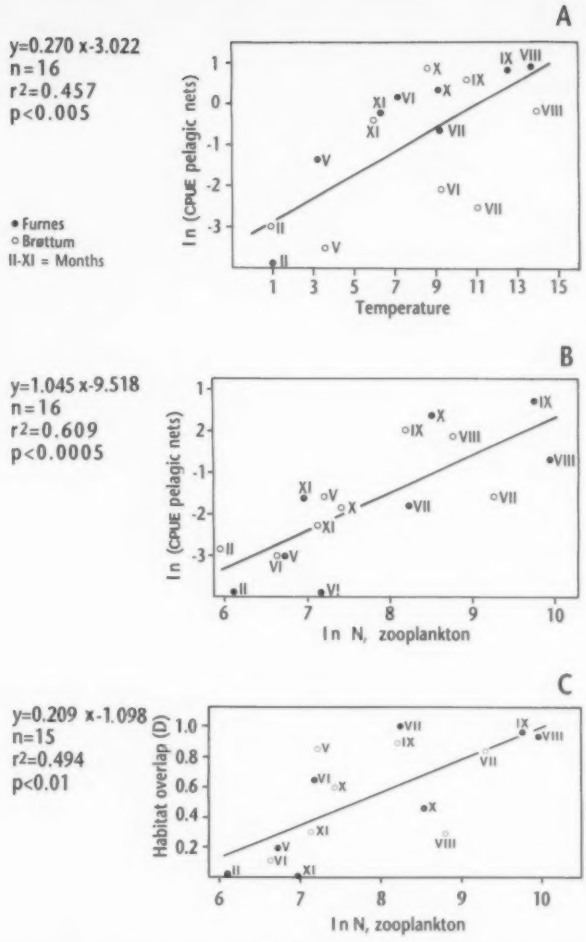

FIG. 5. (A) Linear regression of ln ($\log_e$) CPUE of vendace in pelagic gill nets on water temperature, 0–16 m depth. (B) Linear regression of ln ($\log_e$) CPUE of whitefish in pelagic gill nets on ln ($\log_e$) of number of crustacean zooplankton cubic metre, 0–50 m depth. (C) Linear regression of pelagic habitat overlap between vendace and whitefish (Schoener's (1968) index D) on ln ($\log_e$) of number of crustacean zooplankton cubic metre, 0–50 m depth.

zooplankton than with the epilimnic water temperature (temperature: $r^2 = 0.503$, $p = 0.002$; zooplankton no.: $r^2 = 0.609$, $p = 0.0004$) (Fig. 5B). Water temperature and total number of crustacean zooplankton, however, were intercorrelated ($r^2 = 0.737$, $p = 0.0001$). The two regressions ($CPUE_{whitefish}$ on zooplankton abundance and $CPUE_{vendace}$ on epilimnic water temperature) were not improved by adding water temperature and zooplankton, respectively, as a second independent variable in multiple regression models.

Figure 5B gives the regression of pelagic catch of whitefish over total number of crustacean zooplankton. Points above the regression line represent months where CPUEs were higher than expected from the number of zooplankton, and points below represent months when the catch was lower. It can be noted that the points are below the line in June and July when the abundance of zooplankton was increasing and above the line in September and October after the abundance had passed its maximum and was decreasing. The ln-transformed curves fitted for cladocerans and copepods separately gave $r^2 = 0.568$ and 0.458 ($P < 0.01$), respectively. The pelagic catch also increased with the biomass of crustacean zooplankton (0–50 m), but the fit was not as good as for total numbers ($r^2 = 0.477$, $p < 0.01$).

Neither the pelagic nor the benthic catches of whitefish were significantly ($p > 0.05$) correlated with the abundance or wet weight of insects and molluscs in the benthic habitat (Table 2), the main zoobenthos eaten by the fish (except *P. quadrispinosa* which was not sampled by the Ekman grab). Similiar results ($p > 0.05$) were found for the regressions of whitefish catches on total zoobenthos abundance and wet weight.

In most sampling periods there was a high vertical habitat overlap between whitefish and crustacean zooplankton and vendace and crustacean zooplankton in the pelagic habitat (Table 3). In periods with more than 15 fish caught, Schoener's

TABLE 3. Vertical habitat overlap between whitefish and zooplankton and vendace and zooplankton (Schoener's (1968) index D) in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, May – November 1979 (number of fish in parentheses).

	May	June	July	Aug.	Sept.	Oct.	Nov.
Furnes							
Whitefish	0.521	0.651	0.710	0.715	0.683	0.788	0.253
	(3)	(2)	(11)	(58)	(119)	(83)	(12)
Vendace	0.184	0.893	0.704	0.667	0.679	0.508	0.551
	(17)	(76)	(34)	(289)	(132)	(89)	(48)
Brøttum							
Whitefish	0.216	0.250	0.954	0.418	0.788	0.769	0.577
	(14)	(3)	(15)	(59)	(72)	(11)	(7)
Vendace	0.073	0.670	0.834	0.799	0.908	0.490	0.298
	(2)	(8)	(5)	(57)	(127)	(213)	(45)

TABLE 4. Vertical habitat overlap (Schoener's (1968) index D) between vendace and whitefish in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, February–November 1979.

	Feb.	May	June	July	Aug.	Sept.	Oct.	Nov.
Furnes	0.000	0.202	0.658	0.994	0.952	0.958	0.295	0.133
Brøttum	—	0.857	0.117	0.833	0.297	0.880	0.603	0.298

(1968) index D was lower than 0.5 for whitefish in August at Brøttum and for vendace in May at Furnes and during the spawning run in October and November at Brøttum. Including all periods with more than 10 fish caught of each fish species, there was no significant difference in the habitat overlap of the two fish species, whitefish and vendace, and crustacean zooplankton (Mann–Whitney U-test, $p > 0.05$).

The vertical habitat overlap (Schoener's (1968) index) between whitefish and vendace in the pelagic zone at Furnes was high ($D > 0.6$) during June – September and low during the rest of the sampling period ($D < 0.3$) (Table 4). The index at Brøttum was high during July–October and in May and low in June, August, and November. The habitat overlap increased with increasing number of crustacean zooplankton per cubic metre at 0–50 m depth ($r^2 = 0.494$, $p < 0.01$; Fig. 5C) and with the biomass of zooplankton at 0–50 m depth, although this fit was somewhat lower ($r^2 = 0.462$, $p < 0.01$).

Diet overlap (Schoener's (1968) index) between vendace and whitefish at Furnes was highest in September and lowest in July (Table 5). At Brøttum the diet overlap was highest in August and lowest in October. There was no significant correlation ($p > 0.05$) between diet overlap and habitat overlap or diet overlap and the abundance of different categories of zooplankton.

Discussion

The increase in pelagic gillnet catches of whitefish from May until September indicated a movement of whitefish from epibenthic to pelagic areas. The same movement of whitefish was indicated by density estimates based on echo soundings (T. Lindem, Institute of Physics, University of Oslo, P.O. Box 1048, Blindern, N-0316 Oslo 3, Norway, pers. comm.). The number of pelagic fish of whitefish size (25–35 cm in length) increased from 24 fish·ha^{-1} in May to a maximum of 182 fish·ha^{-1} in September and decreased to a minimum of 21 fish·ha^{-1} in November. During summer, pelagic whitefish probably remained in offshore areas for considerable periods of time

TABLE 5. Diet overlap (Schoener's (1968) index D) between vendace and whitefish in the pelagic zone of the sampling areas Furnes and Brøttum in Mjøsa, July–October 1979.

	July	Aug.	Sept.	Oct.
Furnes	0.076	0.236	0.551	0.289
Brøttum	0.056	0.648	0.516	0.008

because few of the pelagic whitefish caught had remains of zoobenthos in their stomachs. All through the year, whitefish of all length groups stayed in the epibenthic habitat feeding on benthic invertebrates (Sandlund et al. 1991b).

Both gillnet catches and echo soundings indicated that vendace exploit pelagic waters all year round (T. Lindem, pers. comm.). The pelagic CPUEs were more highly correlated with epilimnic temperatures than with the abundance of zooplankton, opposite to what was observed for pelagic whitefish. Therefore, variations in pelagic CPUE of vendace with time may be mainly due to differences in temperature-dependent activity. Vendace probably have a higher preferred temperature than whitefish (Valtonen 1970), although in the literature, evidence supporting this suggestion is meagre.

The CPUE of pelagic whitefish was more highly correlated with both water temperature and biomass of zooplankton than the corresponding relationships for vendace. This was probably because the catch of pelagic whitefish depended both on fish movement between epibenthic and pelagic areas and activity related to water temperature. Vendace, on the other hand, was chiefly exhibiting temperature-dependent activity in the pelagic zone (except for adult fish during autumn on the spawning grounds).

When fish assess the profitability of alternative feeding habitats, a process of learning is probably involved (Werner et al. 1983). Werner and Hall (1988), citing Ehlinger (1986), maintained that when bluegill (*Lepomis macrochirus*) were fed prey from one habitat and switched to prey from another habitat, they suffered nearly a 50% decrease in capture rates on the original prey type, as the new prey type was added to the diet. According to Werner and Hall (1988), learning and search image type phenomena prevented maximum efficiency on both prey types simultaneously.

If learning is involved in the habitat switch of whitefish in Mjøsa, a delay in fish movement relative to the increase in zooplankton abundance was anticipated. This is supported by our results showing that in the period with increasing abundance of zooplankton, CPUE of pelagic whitefish was lower than expected. On the other hand, the CPUE was above the expected value in the period with decreasing abundance of zooplankton. The fish may need some time to learn that food availability has changed, and accommodate to the new situation. In bluegill, Werner et al. (1981) indicated that the time lag between increase in food abundance and habitat change is about 1 wk. A similar time lag was found for Arctic char (*Salvelinus alpinus*) in seven natural lakes in Norway (Langeland et al. 1991). Such a learning mechanism has been described in a simple model called the Relative Payoff Sum (RPS) (Harley 1981; Regelmann 1984). Switching to feeding on zooplankton in the pelagic zone paid off for the first whitefish trying this option when zooplankton densities were high. When zooplankton densities decreased in autumn, whitefish performed an opposite migration back to the, by then, more profitable epibenthic zone. There is, however, still little evidence indicating how learning regulates feeding behaviour of organisms, e.g. to what degree

animals have and use detailed quantitative information about their resources, and to what degree they depend on simpler rules of thumb when they select habitat and prey (Milinski 1984, 1986; Stephens and Krebs 1986).

An alternative to abundance of zooplankton as the explanation to the delay in habitat switch may be that it is influenced by abundance of zoobenthos. We did not, however, find any significant correlation between CPUE of benthic whitefish and the abundance of benthic insects and molluscs which are important food items for the epibenthic whitefish (Sandlund et al. 1991b). A more detailed analysis of all benthos groups might reveal some significant correlations between benthic food supply (e.g. *P. quadrispinosa*) and CPUE of benthic whitefish. We did not, however, have sufficient quantitative zoobenthos data to exploit this possibility.

Ehlinger (1990) found that bluegill selected foraging habitats as a function of the difference in foraging return rates between habitats. The fish spent the longest time in a habitat where the energetic return rate was highest. Our results indicate that within a species the return rate may differ between different size groups. In Mjøsa, medium-sized whitefish (25–35 cm) move into the pelagic zone during summer and autumn whereas smaller and larger fish remain in epibenthic areas. This may be explained by foraging theory, as the smaller fish stay in the more sheltered, epibenthic habitat where predation probably is lower than in the unstructured pelagic zone (Crowder and Cooper 1982; Stephens and Krebs 1986). The large, mobile, epibenthic amphipod *P. quadrispinosa* (8–18 mm in length) is a suitable food item for large whitefish (Næsje 1984; Sandlund et al. 1991b). Feeding on this prey may be more profitable than zooplankton for large fish. There seems to be very little predation on large whitefish in the lake.

In Mjøsa, habitat but not diet overlap between pelagic whitefish and vendace increased with increasing abundance of zooplankton. This might be an indication of exploitative competition, similar to what has been found in sunfishes (Werner and Hall 1979; Werner et al. 1977). Exploitative competition between two species occurs when one species reduces available food supply to a level making the habitat unprofitable for the other species (Werner and Hall 1976, 1977). In Mjøsa the efficient zooplanktivore vendace (Svärdson 1976) may have rendered the pelagic zone an unprofitable feeding habitat for whitefish, except in periods of maximum zooplankton density. Segregation by habitat rather than by diet seems to be the common means of resource partitioning among animal species (Schoener 1974; Schmitt and Coyer 1983). Interference competition, on the other hand, is not easily envisaged in the pelagic zone, as it often involves some aggressive behaviour, e.g. territoriality (Schutz and Northcote 1972; Hindar et al. 1988).

The habitat switches of whitefish and habitat overlap between vendace and whitefish were more highly correlated with number than biomass of zooplankton. These results may indicate that the fish respond to numbers rather than biomass of zooplankton. To be conclusive, however, supporting experimental data are needed.

Whitefish and vendace feed to some extent on the same zooplankton species, and select the same sizes within the species (Sandlund et al. 1987). However, their diet overlap (Schoener's (1968) index *D*) was never above 0.65. This was due to the fact that pelagic whitefish also utilize two other pelagic food sources which are abundant during summer: surface insects and age 0 smelts. Vendace, on the other hand, ate the copepods *L. macrurus* and *E. gracilis* which are not utilized by whitefish. Copepods are generally considered difficult to catch for nonspecialist zooplanktivores (Szlauer 1965; Wright and O'Brien 1984). The difference in trophic morphology (cf. Nikolsky 1963) of the two species reflects the specialist versus the generalist: vendace has a superterminal mouth and dense gillrakers whereas whitefish has a subterminal mouth and sparse gillrakers (mean number of gillrakers 47 and 30, respectively; Sandlund et al. 1987). Whitefish, being the more generalized feeder, performed a habitat shift in relation to the zooplankton abundance whereas vendace, being the more specialized zooplankton feeder, occupied pelagic waters throughout the year.

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Occurrence of the Toxic Phytoflagellate *Prymnesium parvum* and Associated Fish Mortality in a Norwegian Fjord System

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Kaartvedt, S., T. M. Johnsen, D. L. Aksnes, U. Lie, and H. Svendsen. 1991. Occurrence of the toxic phytoflagellate *Prymnesium parvum* and associated fish mortality in a Norwegian fjord system. Can. J. Fish. Aquat. Sci. 48: 2316–2323.

At the end of July 1989, toxin-producing *Prymnesium parvum* was spread through a fjord system in the surge of freshwater released from a hydroelectric power plant. In total, 750 tonnes of Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) died in fish farms. *Prymnesium parvum* germinated in the brackish surface layer of a fjord branch which, during July, was characterized by longer residence time, higher temperatures, and lower nitrogen and silicate concentrations than the rest of the fjord system. Nutrient loading (especially phosphate) from fish farms may, however, have stimulated local growth of the alga. At the time of the first observed fish mortality, the salinity was 5‰ and the temperature 18°C. Pelagic concentrations of *P. parvum* were generally low, with a maximum of 2.2×10^6 cells·L^{-1} found close to a fish farm. Denser concentrations of *P. parvum* were, however, found in association with benthic substrates. Phosphorus limitation was probably important for the production of toxin by *P. parvum*.

À la fin du mois de juillet 1989, *Prymnesium parvum*, algue productrice de toxine, s'est répandue dans un système de fjords à partir de rejets d'eau douce provenant d'une centrale hydroélectrique. Au total, 750 tonnes de saumons de l'Atlantique (*Salmo salar*) et de truites arc-en-ciel (*Oncorhynchus mykiss*) ont péri dans des exploitations piscicoles. *Prymnesium parvum* s'est multiplié dans la couche d'eau saumâtre d'une branche d'un fjord qui, en juillet, se caractérise par un temps de séjour plus long, des températures plus chaudes et des concentrations d'azote et de silicate plus faibles que dans les autres fjords du système. Toutefois, les éléments nutritifs (en particulier, le phosphate) provenant des exploitations piscicoles peuvent avoir stimulé la croissance locale de l'algue. Lorsque les premiers poissons morts ont été observés, la salinité de l'eau était de 5 ‰ et sa température de 18°C. Les concentrations pélagiques de *P. parvum* ont été généralement faibles, la valeur la plus élevée ($2,2 \times 10^6$ cellules·L^{-1}) ayant été observée à proximité d'une exploitation piscicole. Par contre, les concentrations de *P. parvum* ont été plus élevées dans les substrats benthiques. La limitation de phosphore a probablement joué un rôle important dans la production de toxine par *P. parvum*.

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In July–August 1989, 750 tonnes of Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) died in aquaculture enclosures in a fjord system of southwestern Norway. The total economic cost was 35 million Norwegian kr ($5 million (U.S.)). Some mortalities were also reported among free-living fish, but these apparently were not affected as severely (Johnsen et al. 1989; Johannessen 1989).

Mortality of salmon was initially observed in the inner part of the fjord branch Hylsfjorden and thereafter spread outwards through the fjord system (Fig. 1). The fish deaths coincided with the appearance of the prymnesiophycean *Prymnesium parvum*, an oval flagellate about 10 μm long with two flagella and characterized by a short and stiff haptonema. This alga has previously caused fish deaths in brackish fish ponds and other brackish environments in Europe and Asia (Otterstrøm and Steemann Nielsen 1939; Reich and Aschner 1947; Valkanov 1964; Krasnoshchek and Abramovich 1971; Hickel 1976; Comin and Ferrer 1978; Holdway et al. 1978), but to our knowledge, this is the first incident in a large marine (estuarine) system.

At the time of the first observed fish death, the Research Vessel *Håkon Mosby*, with a team of scientists from the University of Bergen, was operating in the fjords to study the effect of onset of freshwater discharge from Hylen hydroelectric power plant, which had been closed during July. Discharge from the power plant, situated at the head of Hylsfjorden (Fig. 1), was initiated the day after the first observed fish mortality in inner Hylsfjorden. Therefore, we were incidentally at the right spot with appropriate equipment. In the present paper, we describe the distribution of *P. parvum* in the fjord system during July–August 1989 and evaluate factors influencing its growth, toxicity, and dispersal in an attempt to identify conditions which led to the event.

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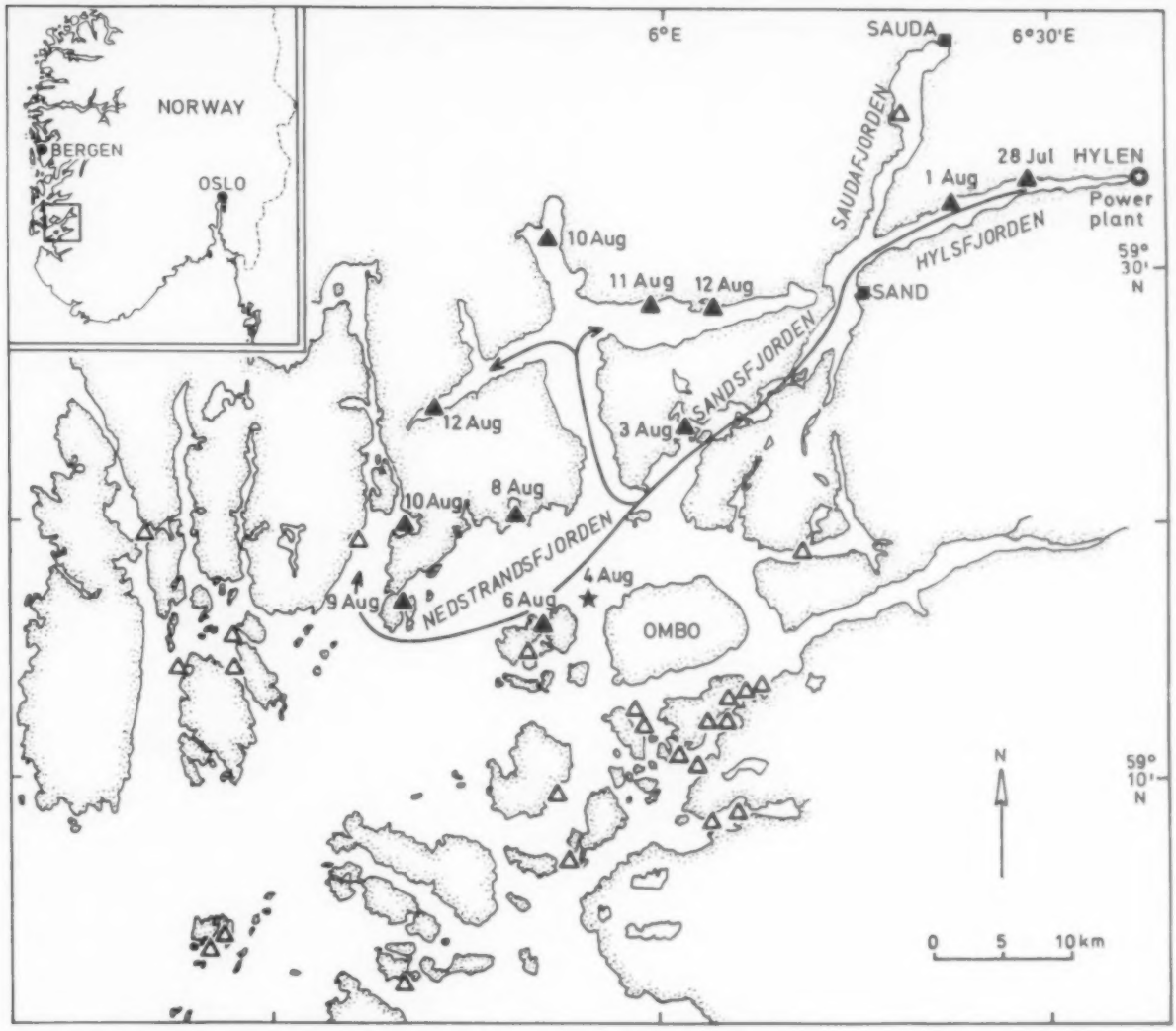

FIG. 1. Time of first observed fish mortality with path of outflowing toxic water indicated. Triangles represent fish farms; star represents well boat. Open triangles show nonaffected fish farms.

Study Area and Methods

The investigation was carried out during 25 July to 6 August 1989, mainly in Hylsfjorden, Saudafjorden, and Sandsfjorden, all of which share a common narrow connection to the outer fjord waters (Fig. 1). Due to high freshwater input and restricted exchange potential, this fjord system is characterized by a marked brackish surface layer (Svendsen 1981; Kaartvedt and Svendsen 1990a). Tidal amplitudes are weak along the southwestern coast of Norway. Amplitude at the mouth of Sandsfjorden is approximately 0.5 m, and tidal current velocities are negligible compared with wind- and freshwater-driven currents (Svendsen 1981; Kaartvedt and Svendsen 1990b).

Currents were measured in Hylsfjorden (Stns. 51, 53, and 55), Saudafjorden (Stn. 58C), and Sandsfjorden (Stns. 64 and 68) by moored Aanderaa and Gytre current metres (Fig. 2). Effects of tides were removed by using a 25-h moving average filter of hourly values.

Transverse recordings of surface (1 m) salinity and temperature were obtained with a Meerestechnik CTD attached to a float which was towed from shore to shore throughout the fjord system. Another Meerestechnik CTD with an oxygen sensor was attached to the hose of a pump during plankton sampling.

Nutrients and phytoplankton samples were obtained with Niskin bottles and a plankton pump. Subsamples (30 mL) for nutrient analysis were preserved with chloroform and refrigerated for later analysis. Weekly sampling of nutrients in the main freshwater sources (Suldalslågen and Hylen power plant) had been undertaken since March 1989. Both live (after *P. parvum* was first identified on 2 August) and Lugol-fixed phytoplankton were examined in samples drawn from the Niskin bottles. Water samples for Chl *a* analysis were taken with the plankton pump. Subsamples (100 mL) were filtered through

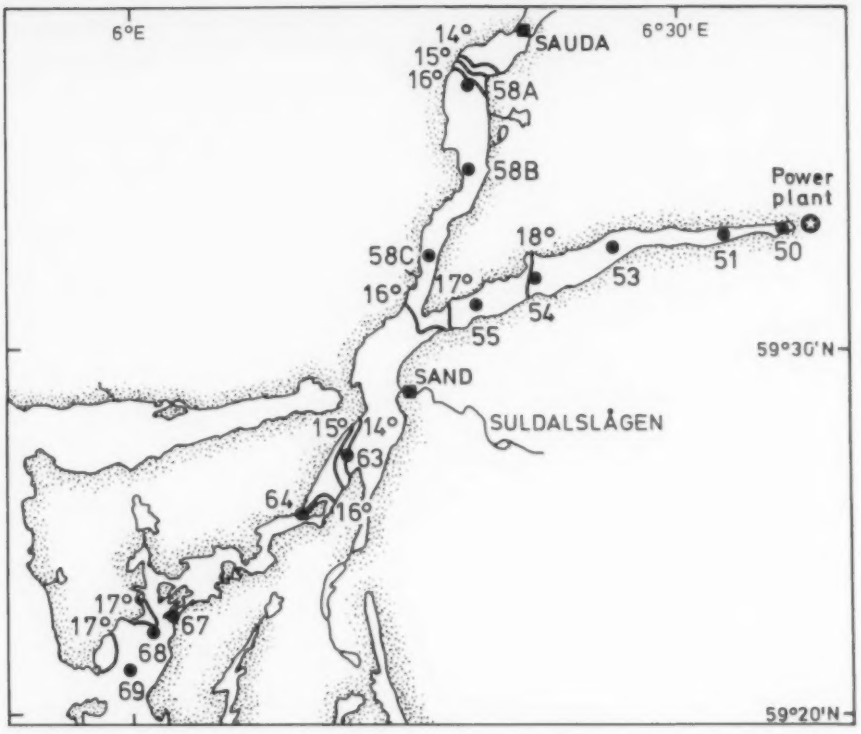

FIG. 2. Sampling stations referred to in the text, and surface temperatures (1 m), 27–28 July 1989.

0.45-μm Sartorius membrane filters. The filters were frozen and later analyzed following the method of Holm-Hansen et al. (1965).

Prymnesium parvum was first observed in a sample from fouling on a fish net, which appeared as a monoculture of the alga. We therefore searched for *P. parvum* on benthic substrates along the shores of the fjord. Benthic sampling was concentrated on macroalgae. The cell numbers obtained from this sampling were not quantitative and could only be used as an indication of high benthic concentrations of the species. On a later cruise (15 August), benthic abundance of *P. parvum* was estimated. Macroalgae covering an area of about 1 m^2 were removed from the substrate and the algae were shaken in a known volume of water to detach affiliated cells of *P. parvum* prior to subsampling for analysis.

Freshwater data (cubic metres per second) were provided for the main freshwater sources by the Norwegian State Power Board.

Results and Discussion

Dispersal of Fish Kills

The first fish mortality was recorded in inner Hylsfjorden on 28 July (Fig. 1). Following the start of discharge from the Hylen power plant on 29 July, mortality spread out through the fjord system. The first pulse of outgoing water was apparently more lethal, but did not affect the adjacent Saudafjorden (Fig. 1). Rain and snowmelt in the mountainous watersheds gave marked increase in runoff at Sauda coincidentally to start of the power plant (Fig. 3). Resulting outward flow of brackish water from

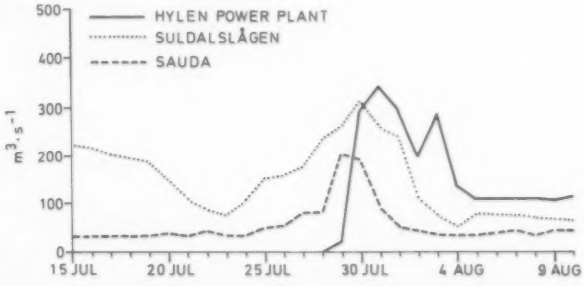

FIG. 3. Freshwater discharge in July–August (daily means) from Suldalslågen, Hylen power plant, and Sauda.

this fjord branch, which on 30 July at least spanned the upper 5 m (not shown), probably reduced intrusion of water from Hylsfjorden into Saudafjorden at that time. Fish died with successively later deaths with increasing distance from Hylsfjorden. While all fish farms located north of the outlet of Sandsfjorden were affected, no mortalities occurred in the large number of fish farms located south of the island of Ombo (Fig. 1). Outflowing water was probably deflected northward by Coriolis force and by the northward heading Norwegian Coastal Current.

Cause of Fish Kills

Prymnesium parvum, which is known as a nuisance alga from other brackish environments, was the most probable agent causing fish mortality and the dispersal of mortality followed

TABLE 1. Numbers of *P. parvum* ($10^6 \cdot L^{-1}$).

		Live samples			Fixed samples					
Station	Depth (m)	Aug. 3	Aug. 5	Aug. 8	July 27	July 29	July 30	Aug. 3	Aug. 4	Aug. 5
Hylsfjorden										
51	0					0.08				
	4					0.23				
53	0		0.50	1.10						
	4		0.00	0.00						
Fish	0					1.61				
farm	1					2.26				
	2					1.68				
	4					1.57				
	6					0.03				
54	1	0.60								
	4	0.06								
	8	0.00								
	12	0.00								
55	0			0.80		0.05	0.55		1.61	
	4					0.05	0.53		0.51	
	6								0.95	
Saudafjorden										
58A	0			0.65						
	4			0.04						
58B	0		0.60		0.00					0.25
	4		0.00							0.14
Sandsfjorden										
63	0			0.50	0.01			0.15		
	4			0.04	0.00			1.55		
64	1	0.70	0.80	0.60						
	4	0.00	0.08	0.00						
	8	0.00		0.00						
	12	0.00		0.00						
69	0		0.08							
	1	0.00								
	4		0.00							
	12	0.00								

the outflowing brackish water containing *P. parvum*. Our results rule out oxygen deficiency as a cause. In Hylsfjorden, 150% saturation was measured just beneath the brackish layer, and the lowest oxygen content observed at the time of first fish mortality was 110% saturation inside net cages in Hylsfjorden. Nitrogen supersaturation or other characteristics of the water from the power plant can also be ruled out, since fish in inner Hylsfjorden started to die prior to the freshwater discharge. No disease was observed in the fish by veterinarians.

Pelagic Distribution of *P. parvum*

In accordance with the chronology of fish kills, the *Prymnesium* distribution data imply that the alga was first established in Hylsfjorden (Table 1). Prior to discharge from the power plant, *P. parvum* was almost exclusively found in this fjord branch, where it was confined to the brackish surface layer. On 29 July, 1 d after the first observed fish mortality, concentrations were 10–40 times higher in the immediate vicinity of the affected fish farm (maximum concentration of 2.2×10^6 cells$\cdot L^{-1}$) than midfjord concentrations in Hylsfjorden (Stns. 51 and 55). The following day, after start of the power plant, concentrations at the outlet of Hylsfjorden (Stn. 55) had increased 10-fold (Table 1), and fish mortality was thereafter observed in the outer part of the fjord branch (Fig. 1). In the beginning of August, *P. parvum* was also present in Sandsfjorden (Stn. 63) and Saudafjorden (Stns. 58A and 58B) (Table 1).

We found low concentrations of *P. parvum* outside Sandsfjorden. Eighteen samples on 4–5 August (mainly from Nedstrandsfjorden; Fig. 1) gave 0 to 0.2×10^6 cells$\cdot L^{-1}$. Later, during the main fish kills outside Sandsfjorden, outflowing brackish water generally contained *P. parvum* in pelagic concentrations of 0.5 to 1.5×10^6 cells$\cdot L^{-1}$ (J. Aure, Institute of Marine Research, Bergen, pers. comm.).

Algal Transport as Revealed from Chl *a* and Water Movements

Strong mixing between cold freshwater and fjord water took place near the power plant outlet in inner Hylsfjorden (Stn. 50)

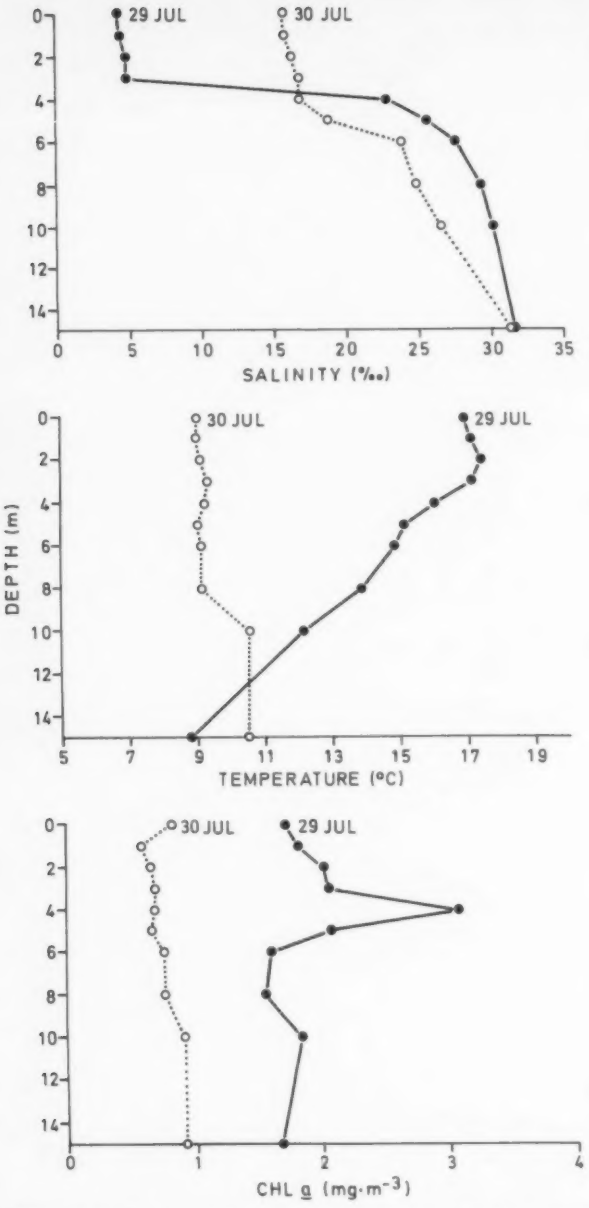

FIG. 4. Salinity, temperature, and Chl *a* at the head of Hylsfjorden (Stn. 50) prior to and after the start of the power plant.

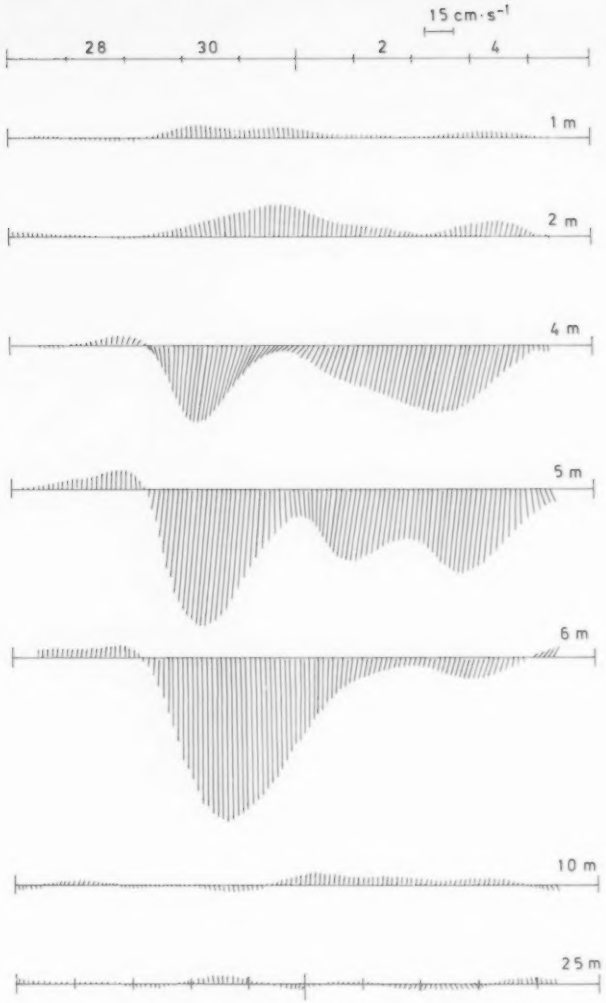

FIG. 5. Current velocities in the inner part of Hylsfjorden (Stn. 51) showing low velocities prior to the start of the power plant and an outwardly directed current beneath the surface layer in response to freshwater discharge from the power plant. The horizontal axis represents dates in July–August 1989. Downward lines represent outgoing currents and upward lines represent ingoing currents.

at the onset of the discharge from the Hylen power plant (Fig. 4). Temperature decreased by 8°C and salinity increased by 12‰ in the upper layer of the mixing zone. This new water mass (henceforth denoted discharge water mass; DWM) consequently had higher density than the surface water elsewhere in the fjord system, and a normal estuarine circulation was not generated. Instead, the DWM submerged beneath the existing surface water in a clearly separate frontal zone in inner Hylsfjorden (located between Stns. 50 and 51) and proceeded as an outwardly directed current at between 3 and 8 m (Fig. 5 and 6).

Algae were transported outwards with the freshwater-driven currents, and Chl *a* decreased considerably at the head of the fjord (Stn. 50) from 29 to 30 July (Fig. 4). Further out in Hylsfjorden, the DWM appeared as a cold core with reduced Chl *a* values (Fig. 6). This cold-water core was observed throughout Hylsfjorden, but on 30 July there were no recognizable effects further out in the fjord system.

Observations on 2 August demonstrated that relatively low-salinity water flowed out of the fjord. At the outlet of Sandsfjorden, the salinity was 17‰ towards the northern shore, i.e. 10‰ lower than 5 d earlier (see later). Current meters at the outlet of Sandsfjorden revealed outgoing currents in the upper 10 m.

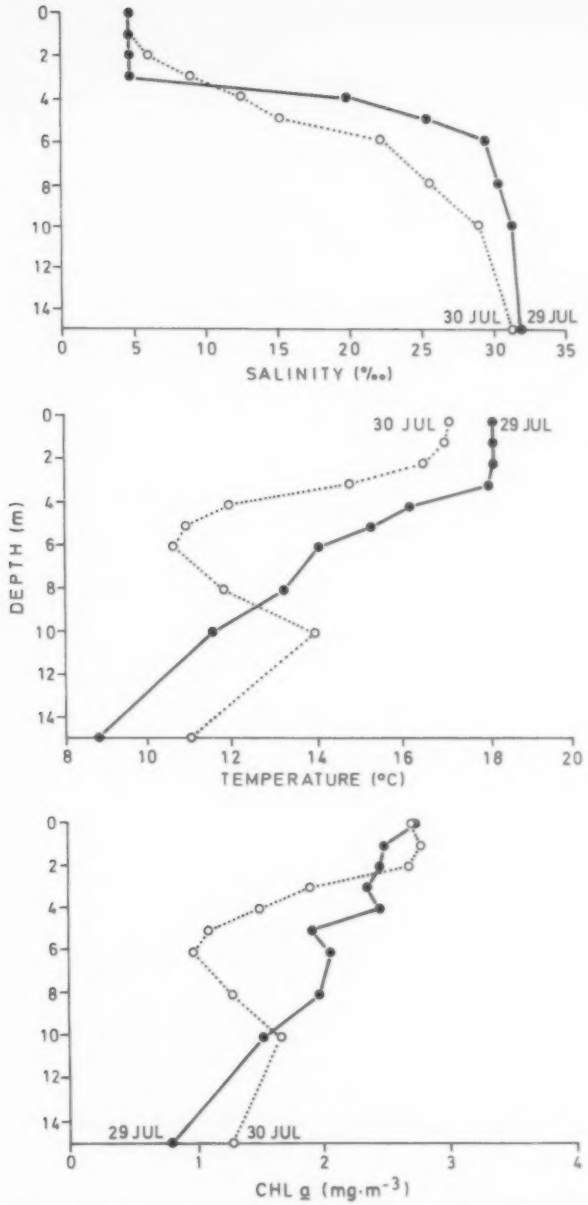

FIG. 6. Salinity, temperature, and Chl *a* near the location of first fish mortality (St. 53) prior to and after the start of the power plant. The discharge water mass (DWM) is recognized as a cold core with reduced Chl *a* content.

Algal Concentrations and Fish Kills

Pelagic algal concentrations were an order of magnitude lower than generally found in association with fish kills, and Holdway et al. (1978) stated that 10^7–10^8 cells·L^{-1} is necessary to provoke mortality. However, we repeatedly observed high concentrations of *P. parvum* from benthic samples, a previously unreported association (Johnsen and Lein 1989). *Prymnesium parvum* seemed to be specifically associated with the green macroalgae *Cladophora* spp. By shaking *Cladophora* in water, concentrations up to 400×10^6 cells·L^{-1} were obtained. Estimates based on a sample taken from 1 m^2 of shoreline (15 August) densely covered with *Cladophora* gave an abundance of 10^{10} cells·m^{-2}.

Toxic pockets of water, without high concentrations of cells, may have developed nearshore or at other benthic accumulations of *P. parvum*, since *P. parvum* excretes its toxins into the surrounding water (Otterstrøm and Steemann Nielsen 1939; Shilo and Aschner 1953). It is likely that accumulation of *P. parvum* took place on nets of fish cages, which may have caused toxic waters in the vicinity of large concentrations of fish. *Prymnesium parvum* had a high affinity for attachment to benthic substrate, and repeated fouling of fish nets (*P. parvum*) was observed even when these had been in the water for only a few hours. Accumulations on fish cages cannot, however, explain all incidences of mortality in the fjord system, as salmon also occasionally died in boats used to monitor the distribution of poisonous water (Institute of Marine Research, Bergen).

Phosphorus-limited growth was probably essential for the poisonous effect of *P. parvum*. With phosphorus limitation, toxicity increases with a factor of 10–20 (Shilo 1967), and without phosphorus limitation, the species may be found in large concentrations without affecting fish (Holdway et al. 1978; Shilo 1981). The freshwater supplying the brackish fjord water with nutrients had relatively high concentrations of silicate and nitrate, but low concentrations of phosphate (Table 2). The N:P values in the surface layer of the fjord system accordingly were much higher than the Redfield ratio of 16 (Table 3). Phosphorus limitation in the brackish layer was also indicated by high phosphatase activity in August 1989 (T. F. Thingstad, Department of Microbiology and Plant Physiology, University of Bergen, pers. comm.).

TABLE 2. Concentrations (μM) of silicate (S), nitrate (N), and inorganic phosphate (P) in the main freshwater sources during spring and summer 1989. Phosphate values were below the detection level of 0.05. Number of samples is given by *n*.

	n	S	N	P
Suldalslågen, March–July	17	15.0	12.6	<0.05
Hylen power plant, March–June	12	13.8	10.3	<0.05

TABLE 3. Average ratios between nitrate and inorganic phosphate (N:P) with 95% confidence intervals showing values much higher than the Redfield ratio in freshwater and in surface waters inside the fjord system. When phosphate was below the detection level, the value was set at 0.05 μM. Results from previous investigations are given, where data from all stations and times of the year are combined. Number of samples is given by *n*.

	n	N:P
Surface water		
Inside Sandsfjorden, 1987–89	102	47 ± 6
Inside Sandsfjorden, July–August 1989	18	64 ± 10
Outside Sandsfjorden, 1987–89	50	12 ± 3
Freshwater		
Suldalslågen, 1988–89	18	173 ± 42
Hylen power plant, 1988–89	16	143 ± 28
Other sources, 1988–89	10	165 ± 134

Conditions for Growth of *P. parvum*

In determining favorable conditions for *P. parvum* to multiply, it is essential to identify ecological characteristics which distinguished Hylsfjorden (where *P. parvum* apparently was first established) from the rest of the fjord system. These include the residence time, temperature, and nutrient dynamics of the brackish water. Human impacts on the environment comprise aquaculture, which expanded markedly in the 1980s, and the establishment of the Hylen power plant which started operating in 1980.

Salinity

All fjord branches were characterized by a conspicuous brackish surface layer. During the end of July (27–28), surface salinities were 4–5‰ through most of the fjord system. In outer regions (outside Stn. 64), surface salinity increased seaward and was 27‰ at the outlet of Sandsfjorden (Stn. 69). The low salinity of the brackish layer probably was important for the occurrence of *P. parvum*. The salinity of the brackish layer in July–August 1989 was similar to that found in many other systems where *P. parvum* has caused fish mortalities (Otterstrøm and Steemann Nielsen 1939; Krasnoshchek et al. 1972; Hickel 1976; Comin and Ferrer 1978; Holdway et al. 1978), and laboratory experiments with *P. parvum* from the fjord system showed that growth was inhibited in salinities exceeding 20‰ (Kaartvedt et al. 1990). The salinity alone, however, can neither explain why the event was initiated in Hylsfjorden nor why *P. parvum* appeared in 1989. There were no differences in salinity between the fjord branches, and results from baseline studies prior to the hydroelectric development show nearly identical surface salinities (Svendsen 1981; Kaartvedt et al. 1990).

Temperature

The highest temperature (18.5°C) was recorded in Hylsfjorden (Fig. 2), where the surface water represents a backwater when the power plant is shut down. *Prymnesium parvum* thrives in "a mild climate" (Collins 1978), and the high temperatures in Hylsfjorden in July 1989 may have favored the alga in this fjord branch compared with the colder water in other parts of the fjord system. However, while *P. parvum* flourishes in warmwater fish ponds in Israel (e.g. Shilo 1971), blooms with associated fish deaths have also been reported in waters with temperatures down to 5°C (Otterstrøm and Steemann Nielsen 1939; Krasnoshchek and Abramovich 1971).

Nutrients

Nutrient concentrations in the "old" brackish layer of Hylsfjorden were much lower than in Sandsfjorden (Fig. 7) and Saudafjorden, which received large amounts of nitrate and silicate from river runoff. Phosphate levels of the brackish water were, on the other hand, low throughout the fjord system (0.05–0.1 μM). The two fish farms in Hylsfjorden do, however, represent major nutrient sources. Fertilization associated with fish farming seems to create favorable conditions for *P. parvum* (Collins 1978; Holdway et al. 1978), and *P. parvum* has repeatedly been found in association with fish farming in brackish water (Reich and Aschner 1947; Shilo 1967, 1971; Krasnoshchek and Abramovich 1971; Krasnoshchek et al. 1972; Hickel 1976). Estimated phosphorus loading from the two fish farms in Hylsfjorden is about 10 kg water-soluble phosphate·d^{-1} (Kaartvedt et al. 1990). This amount of phosphate could theoretically lead to a daily increase of 10^{16} *P. parvum* cells, given the same phosphorus cell content as in *Chrysochromulina polylepis* (Dahl et al. 1990). Averaged over the entire Hylsfjorden,

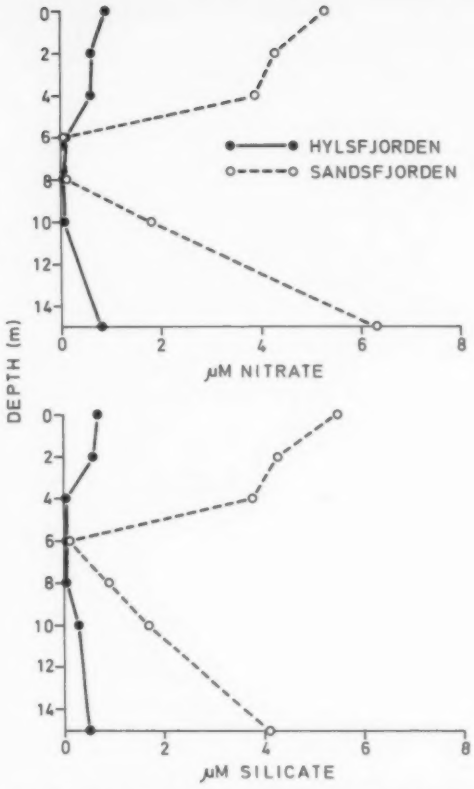

FIG. 7. Nitrate and silicate levels in Hylsfjorden (Stn. 51; 29 July) and Sandsfjorden (Stn. 63; 27 July) prior to initiation of freshwater discharge from the Hylen power plant. Biological consumption had nearly depleted the nutrient reservoir in the "old" Hylsfjord water.

this corresponds to a daily new production of 10^9–10^{10} cells·m^{-2}, and an accumulated effect involving recycling of nutrients may be expected in the backwaters of this fjord branch. While only a portion of the phosphorus loading will provide growth of *P. parvum*, it is also unrealistic to average the nutrient supply over the entire fjord branch. Currents in Hylsfjorden were weak in July prior to the start of the power plant (e.g. Fig. 5), which enables local establishment of the alga without substantial advective loss and facilitates local utilization of nutrient sources. The results from 29 July, when 10–40 times higher concentrations of *P. parvum* were found close to the fish farm than at midfjord stations (Table 1), substantiate this argument. Benthic settlement of *P. parvum* may also have facilitated increased efficiency in utilization of nutrient release from the fish farms.

Also, discharge from the power plant increases the nutrient input to Hylsfjorden. The power plant is usually not operated in June–July, but in June 1989, extra silicate and nitrate were supplied due to ancillary operation of the plant. The freshwater discharge, however, makes the nutrient regime of this fjord branch more similar to the rest of the fjord system. Actually, the low silicate level which develops in Hylsfjorden when the power plant is shut down should favor flagellates over diatoms in this part of the fjord system (Officer and Ryther 1980).

Conclusion

Prymnesium parvum germinated in the low-salinity water of a fjord branch characterized by long residence time of the brackish water. This led to relatively high temperatures, depletion in nitrogen and silicate derived from the freshwater, and low advective loss of algae. Low exchange rates and benthic association may also have facilitated an accumulated effect of continuous nutrient supply from fish farms. *Prymnesium parvum* was advected outwards in currents generated by controlled freshwater discharge from a hydroelectric power plant, which was initiated at the time of the first observed fish mortality. Coincident large runoff from other sources contributed to far-reaching dispersal of the alga out of the fjord system. Phosphorus-limited growth probably was important for the toxicity of the alga.

The present case represents the first report of fish kill by *P. parvum* in a large marine (estuarine) ecosystem and the first example of extensive growth of this phytoflagellate in association with benthic substrate. This extension in type of environment and of growth mode suggests that the alga may become a threat to an expanding marine aquaculture industry, as it has proved to be in inland brackish fish ponds. Our results give a clue to one type of environment which may favor outbreaks. However, the peculiar set of ecological conditions of the microenvironment in which the core population of *P. parvum* developed was in many respects rather similar to previous described locations and atypic to most marine aquaculture sites. In this particular fjord system, the development of future incidents possibly can be manipulated by human control of the freshwater discharge.

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Use of Size–Frequency Data to Estimate the Age Composition of Crayfish Populations

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Age-classes in crayfish populations can be determined from size–frequency data provided four tenets are adhered to: (1) only crayfish collected from areas of rock substrate are used; (2) trapping data are excluded; (3) species do not have longevities exceeding about 4 yr; and most importantly, (4) sample sizes are greater than about 200. Studies that have failed to follow these guidelines have met with limited success in dissecting mixed frequency distributions. Further, three validation procedures must be undertaken: (1) temporal replication within molting events to measure the precision of both data collection and size–frequency analysis; (2) corroboration with known-age crayfish from either field recaptures or laboratory molt increments; and (3) concordance with independent analysis of the mean size at onset of sexual maturity. When these checks support the size–frequency results, population age composition and analyses of rates of growth or mortality can be considered reliable.

Les classes d'âge dans les populations d'écrevisses peuvent être déterminées à partir des données sur la taille et la fréquence à condition de respecter quatre principes : 1) seules les écrevisses récoltées dans les zones à substrat rocheux sont utilisées; 2) les données de piégeage sont exclues; 3) les espèces étudiées ne doivent pas avoir une longévité supérieure à environ quatre ans; et surtout, 4) la taille des échantillons doit être supérieure à 200. Lorsque ces principes n'ont pas été respectés, on n'a que partiellement réussi à séparer les distributions de fréquence hétérogènes. Outre ces principes, il faut appliquer trois méthodes de validation : 1) réplication temporel pour les événements de mue afin de mesurer la précision de la collecte de données et de l'analyse de la taille et de la fréquence; 2) confirmation à partir d'écrevisses d'âge connu par recapture en nature ou par observation en laboratoire des incréments de mue; et 3) concordance des résultats avec l'analyse indépendante de la taille moyenne au début de la maturité sexuelle. Lorsque toutes ces vérifications confirment les résultats relatifs à la taille et à la fréquence, les données relatives à la composition des classes d'âge de la population et les analyses des taux de croissance et de mortalité peuvent être considérés comme fiables.

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The absence of hard body structures with annuli severely complicates the estimation of age, growth, and mortality for such organisms as tropical fish and all crustaceans. Consequently, workers must rely upon indirect methods to estimate age and, for invertebrates, molt increments and frequencies. The use of size–frequency distributions to distinguish among modal size groups from which to estimate demographic parameters such as growth and mortality rates is a long-established tradition in aquatic sciences. Because crustaceans have a noncontinuous stepwise pattern of growth, such procedures are commonly (although it may be argued, uncritically) applied to studies of these organisms.

Polymodal frequency distributions of freshwater crayfish have been interpreted by a variety of statistical techniques since early researchers such as Van Deventer (1937) followed the progression of modal sizes through time. Hopkins (1966, 1967), St. John (1976), and France (1985) used the probability plot method of Harding (1949) and Cassie (1954); Flint (1975) used the iterative parabola technique of Tanaka (1962); and Somers (1987) used the mathematical programs of Macdonald and Pitcher (1979). These methods share a graphical basis for dissecting mixed distributions into their component parts and then interpreting the separate modes as revealing individual age-groups. Recently, Davies (1989) presented some data which seem to contradict this technique, and as a result, led him to abandon its use.

The purpose of this paper is to defend the utility of size–frequency data for estimating the age composition of crayfish populations by (a) suggesting three validation procedures which should be examined prior to acceptance of any such analyses and (b) identifying four operational caveats which are commonly ignored. Because Davies (1989) criticized the validity of determining age structure from population length–frequency data, he also seriously questioned the demographic parameters previously estimated for *Orconectes virilis* in the Experimental Lakes Area (ELA) (France 1985; France and Graham 1985). Therefore, the background information from France (1983)

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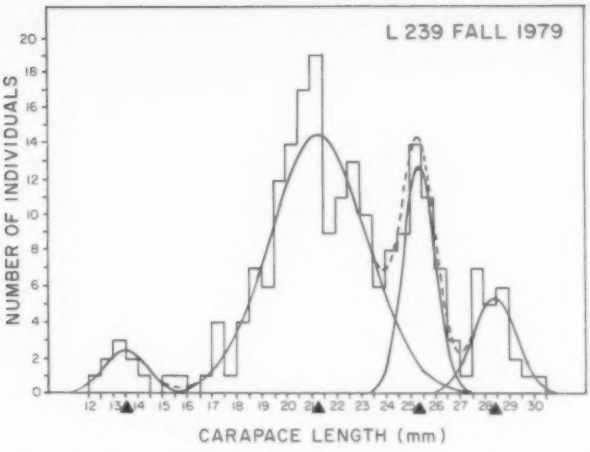

FIG. 1. Mixture analysis applied to a sample of 221 crayfish from Lake 239 using the procedure of Macdonald and Pitcher (1979). Solid (lower) curves represent age-groups; broken (upper) curves represent the fitted total mixture over all age-groups which should be compared with the histogram. Positioning of triangles denotes age-group mean sizes.

upon which these demographic parameters are based will be critically reevaluated.

Graphical and Mathematical Methods

Both graphical (Cassie 1954) and computer-based mathematical (Macdonald and Pitcher 1979) methods have been developed to estimate demographic parameters of populations from size–frequency distributions. Both methods assume that populations can be described as mixtures of normal (or in some cases log-normal) distributions which can be decomposed into many normal distributions representing single age-classes. Graphical methods estimate the parameters of a given age-class from a region of the overall size distribution in which the effects of other age-classes are negligible. In contrast, mathematical methods optimize the fit of the distribution function defined by the parameters to the size–frequency histogram (Macdonald and Pitcher 1979; Grant et al. 1987).

Hopkins (1966, 1967), St. John (1976), and France (1985) used the probit graphical method of Cassie (1954) to differentiate age components. Somers (1987), however, opted for the mathematical optimization procedure of Macdonald and Pitcher (1979) because it reduces the subjective element in analysis due to the difficulty in detecting inflection points required by the graphical method. Users of the mathematical optimization procedure have stated that "the interpretation of the graphs still leaves much to the imagination of the user" such that the results of such probit methods "are not reproducible" (Macdonald and Pitcher 1979) and are therefore "of limited usefulness, except when the age groups are very well separated and sample sizes are very large" (Grant et al. 1987). Because the rest of this paper relies upon results generated by both methods, it is important to compare their performances to determine whether the graphical technique can reproduce the more objective mathematical results.

Therefore, to reevaluate the conclusions of France (1985) and France and Graham (1985), the results of 10 randomly selected frequency distributions (originating from four lakes and spanning spring, summer, and autumn collection periods) were independently reanalyzed (by J.H.) using Macdonald and Pitcher's (1979) programs (e.g. Fig. 1) with no knowledge of the modal sizes previously assigned (by R.F.) using Cassie's graphical technique (cf. France 1983). Each size distribution was analyzed three times using different starting values to ensure that the solutions were unique and not dependent on starting values. No constraints such as a constant coefficient of variation were imposed when estimating parameters. Solutions were accepted when χ^2 values were small and standard errors were low relative to the parameter estimates.

The estimates of crayfish mean lengths produced using Cassie's (1954) and Macdonald and Pitcher's (1979) methods are very similar (Fig. 2). The largest deviations from the line of equality occurred in the oldest age-classes because the number of large individuals in the samples was small. The largest deviations were the result of lower estimates from France 1985). This is not surprising, as it is notoriously difficult to determine the precise location of the infection points used to separate older, slower growing age-groups using Cassie's method. Neither method produced estimates which were consistently higher or lower than the other. Differences averaged only 0.22 ± 0.19 (SD) mm, which is less than 6% of the mean size differences observed among equal-aged crayfish in ELA lakes (France 1985).

We do not mean to imply an endorsement in the use of graphical methods when mathematical optimization programs are nowadays readily available. Not only are the later procedures superior in reducing (although it must be noted, never completely eliminating) subjectivity, but their great strength lies in the fact that they allow true confidence limits to be placed around the parameter estimates (Grant et al. 1987; Grant 1989). Such a procedure is preferable to having to rely upon the substantially statistically weaker fiducial limits (see Hodson et al. 1977) which are all that is possible based on the cumulative probit procedures of the graphical method. These confidence limits are important in providing a warning when the estimates become unstable and therefore unreliable. We have shown that, provided the researcher has a good knowledge of the expected longevity of the crayfish populations, the subjective graphical methods may not be as fallacious as has sometimes been suggested (e.g. Davies 1989). Moreover, there are independent ways of validating the age-classes derived by both procedures which need always to be considered.

Validation Procedures

The validity and general acceptance of any method should be judged by both the precision and accuracy of its performance. It is imperative that performance be tested in each particular study before size–frequency data can be accepted to reflect population structure (Grant et al. 1987).

Sampling Replication

Independent sampling remains a powerful validation procedure. For example, no increase in *O. virilis* size occurred during the 6-mo winter period at ELA as would be expected for this species (Weagle and Ozburn 1972). In particular, SCUBA collections in Lake 223 during October 15–22, 1979, produced the following mean sizes: age 0, 12.8 mm; age I, 19.5 mm; age II, 24.1 mm; and age III, 28.4 mm (France 1985). When the

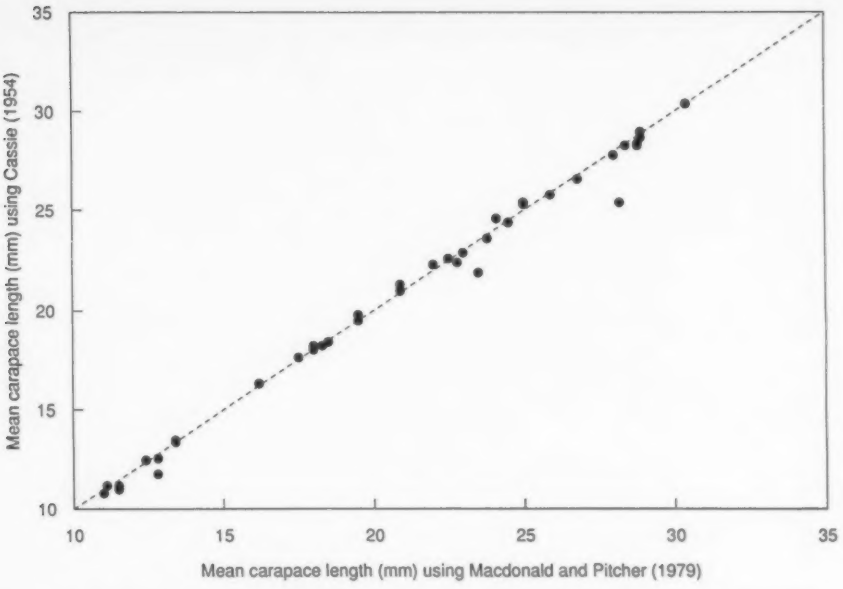

FIG. 2. Comparison of estimated modal mean sizes independently obtained from mixed frequency distributions using Macdonald and Pitcher's (1979) mathematical optimization procedure and Cassie's (1954) subjective graphical method.

same population was sampled the following spring on May 18–19, 1980, there were no significant differences (t-tests, p's > 0.05) in the mean lengths between equivalent age components: age 0 crayfish (now represented as age I), 12.4 mm; age II, 19.5 mm; age III, 24.5 mm; and age IV (formerly age group III), 28.9 mm (France 1983). It was on this basis that we combined these two collections to provide the dataset used in the subsequent section to examine the effects of sample size on the detection of age-classes and estimation of demographics. This overwinter comparison was consistent for other ELA lakes and therefore validated the precision of both data collection and analytical techniques, thereby supporting conclusions made about size differences observed among lakes (France 1985).

Known-Age Verification

Even though the consequences can be severe, many biologists continue to negelect the critical study of age validation (Beamish and McFarlane 1983). Age-class modes estimated from size–frequency histograms should be verified with data on known-age recaptured, or laboratory-molted, organisms (Jones 1981); otherwise, calculations of growth rates may be tenuous (Somers 1987). Such accuracy checks have been undertaken by Momot (1967), Hopkins (1967), Flint (1975), France (1983), and Hazlett and Rittschof (1985). An aging method which is independent of size is the best validation procedure. For example, Momot (1967), using mark–recapture data on a Michigan population of *O. virilis*, found that while young-of-the-year (age 0) and yearlings (age I) formed distinct groupings, age II and III individuals overlapped, producing an accuracy of 80% in correct aging from inspection of size–frequency data.

Comparisons can be made between the molt increment data for individual *O. virilis* from Lake 240 held captive during their molt (Fig. 3) with size changes observed within each "age"

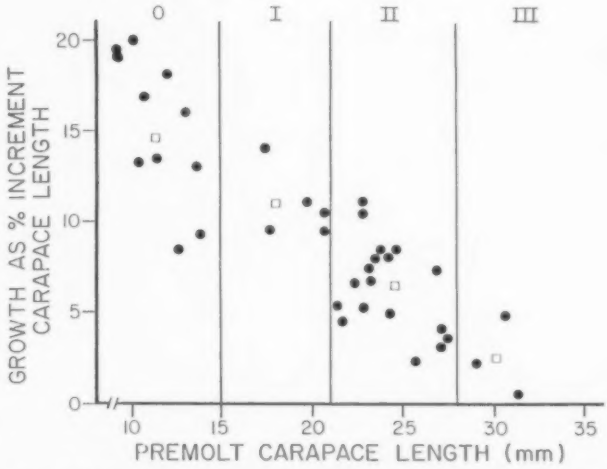

FIG. 3. Growth increment per molt as a percentage of original carapace length for Lake 240 crayfish. Open squares represent mean percentage growth increment for the various age-classes. These data are used to derive the relationship postmolt CL = 2.37 + 0.97 premolt CL, $r = 0.99$, $n = 39$ (France 1985, p. 1098).

component of the Lake 240 population in the field during 1980, as well as the "annual" intermodal distances observed between any of the peaks in the Lake 240 size–frequency histogram. In such cases, the empirically derived number of molts (France 1985) agreed very closely with life history data for this species from other regions (Aiken 1967; Weagle and Ozburn 1972).

Size at Maturity

If the modal age/lengths used to calculate growth rates have validity, then there should be a concordance between these

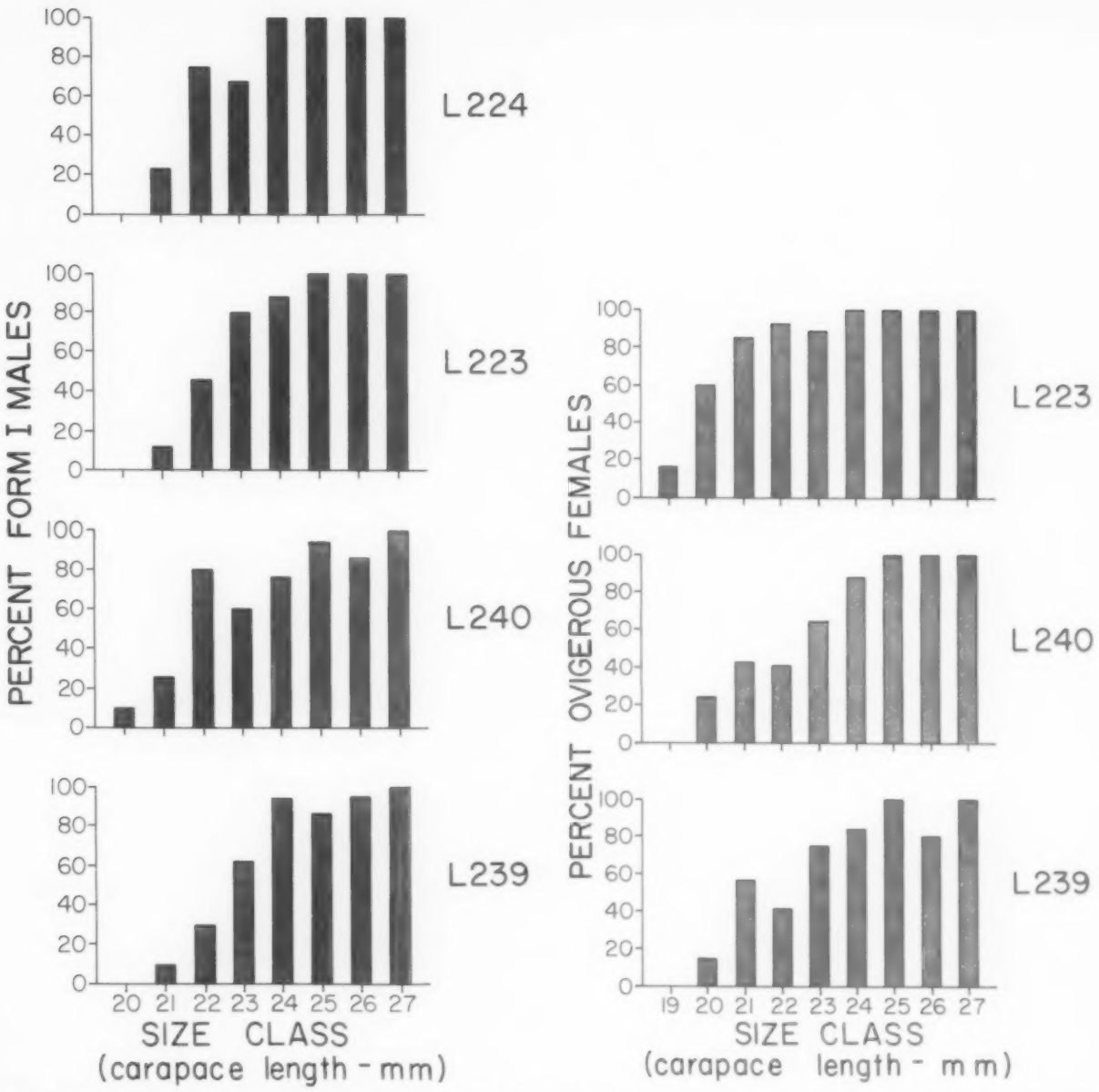

FIG. 4. Percentage variation of sexual maturity with size in ELA male and female crayfish populations during 1979 arranged in order from top to bottom of increasing growth rate determined in France (1985). Compare these figures with the mean carapace lengths at onset of sexual maturity presented in France (1985, table 2).

growth rates and a ranking of interpopulation body size differences derived independently from size–frequency analysis. The relationship between percent of mature females or form I males and carapace length (Fig. 4) permits calculation of the mean size at onset of sexual maturity (SOM). According to this technique, a population exposed to environmental factors that are unfavorable to growth will decrease its SOM relative to another unaffected population (Wenner et al. 1974). France (1985) found the SOM to be a sensitive index for discriminating *O. virilis* growth differences among ELA lakes and between years within a lake. These results, together with those of Flint and Goldman (1977), Huner and Romaire (1978), Price and Payne (1984), Somers (1987), and Olvoch (1990), support the use of SOM for assessing size differences between discrete crayfish populations where detailed assessments of growth rates may be infeasible because of limited data. In those situations such as the present case where the interpopulation rankings of size–frequency growth analyses and the SOM indices are strongly correlated, conclusions reached on the basis of size–frequency derived age composition can be considered reliable.

Operational Caveats

Sample Size

As Jones (1981) stated, "size–frequency analysis by graphical means is extremely difficult to apply satisfactorily when the data are few" (see also Taylor 1965). Macdonald and Pitcher (1979) recommended a minimum sample size of at least 50 individuals per age-class. We believe that no single factor has contributed more to the unjustified abandonment of the size–frequency procedure for estimating crayfish population structure than inadequate sample sizes. Consideration of sample size alone may be sufficient to explain the discordant results reported in the literature with respect to ability in discriminating modal size groupings: (1) success: France (1985; n = 193–294, mean = 237) and Hopkins (1966; n = 100–400); (2) moderate success: Hopkins (1967, n = 61–180); and failure: Davies (1989; n = 21–139, mean = 73) and Jones (1981; n = 74).

To investigate the reliability of different sample sizes in detecting age-classes, we performed the following iterative resampling experiment. Data from collections in late autumn 1979 and early spring 1980 in Lake 223 were combined (see previous section on validation through replication) to yield an initial representative sample of 587 individuals. From this, subsamples of different sizes (500, 400, 300, 200, 100, 75, 50, and 25) were randomly drawn with replacement. We produced 100 replicates for each subsample and averaged them to the nearest integer (Fig. 5). Each average subsample was then analyzed with Macdonald and Pitcher's (1979) method. We attempted to fit one and two components to the small (n = 25, 50, and 75) datasets, one to four components to the n = 100 dataset, and three, four, and five components to datasets of 200 and more (e.g. Fig. 6) based on an initial visual assessment of the histograms. Each dataset was analyzed three times using different initial values to ensure that solutions were not dependent on starting values. As before, solutions were obtained without imposing constraints (e.g. a constant CV) on the parameter estimates.

Following Grant et al.'s (1987) advice, the means and standard deviations and their standard errors of the frequency components are shown in Table 1. The best solutions for the smallest datasets (n = 25, 50, and 75) were obtained through fitting one component (Fig. 6). When two components were fitted to these data, similar χ^2 values were obtained but the standard errors of the second component were generally equivalent to the parameter estimates. Although three components were fitted to the n = 100 data (Fig. 6), the standard errors of the third component were large. However, standard errors for two- and four-component fits were higher. At sample sizes of 200 and greater, four components provided the best fit to the data (e.g. Fig. 6). When either three or five components were fitted, comparable χ^2 values were obtained. However, with three components, the last component completely overlapped the second component and partially overlapped the first component. In contrast, when five components were fitted, the standard errors of at least two

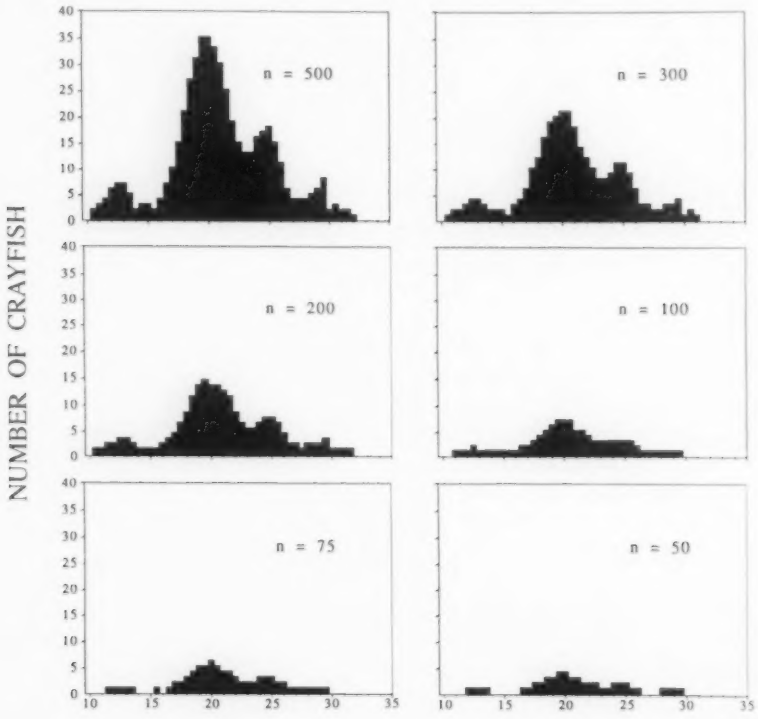

FIG. 5. Randomly resampled datasets based on averages of 100 replicates of 500, 300, 200, 100, 75, and 50 crayfish from combined late autumn 1979 and early spring 1980 collections in Lake 223.

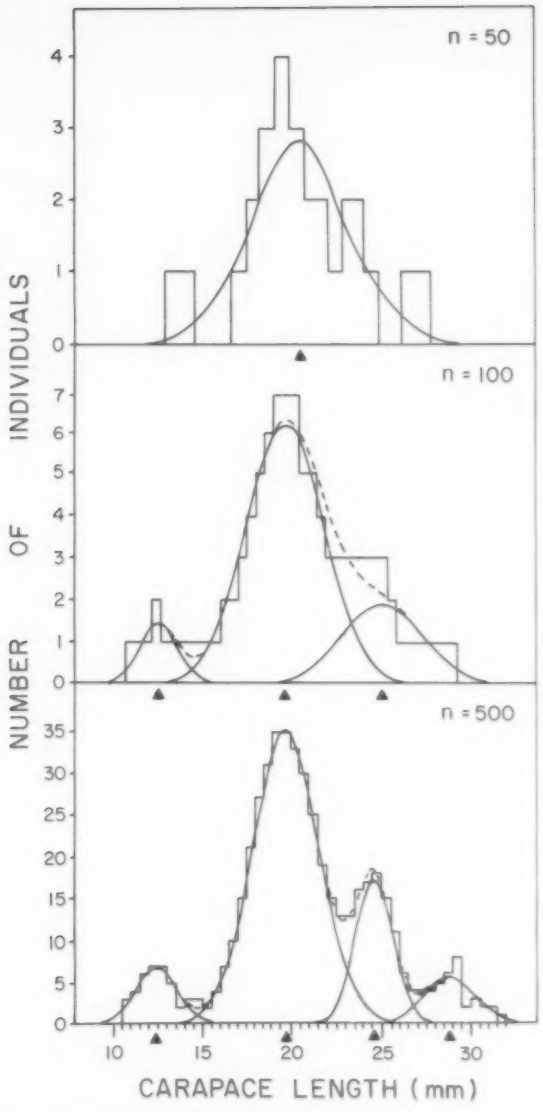

FIG. 6. Mixture analysis applied to samples of 50, 100, and 500 crayfish from Fig. 5 using the procedure of Macdonald and Pitcher (1979). Triangles denote age-group mean sizes.

components (usually from among the middle three) became unacceptably large, being either the same magnitude or in most cases greater than the parmeter being estimated, indicating that there is not enough information in the histogram to estimate those parameter(s). The standard errors of the parameter estimates declined as sample size increased from 200 to 500, indicating that the ability to clearly distinguish four age-classes improved with increasing sample size. This was also noted by Grant et al. (1987) in their analysis of simulated data sets.

What are the mininum sample sizes necessary for derivation of demographic parameters? Obviously, datasets smaller than about 200, and most particularly, less than 100, are inadequate for discriminating even the number of age components existing in the sample. Mean carapace lengths were essentially identical over the sample size range from 500 to 200 (although, as mentioned, precision diminished). Consequently, a minimum sample size of at least 200 individuals is deemed essential for calculation of accurate growth rates for these crayfish populations. The proportional distribution of individuals within the four defined age-classes (Table 2) showed little change over the sample size range of 500 to 200 (although, as with mean sizes, the standard errors about the estimates increased slightly). Calculations of population mortality rates based on catch curve statistics (see France and Graham 1985) will therefore be relatively constant with sample sizes exceeding 200 for these subpopulations.

Because our analysis was based on the average distribution of 100 replicates, the conclusion of a minimum sample size of 200 may be conservative (P. Olesiuk, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada, pers. comm.). This is because we have underestimated the random error that would be inherent to each of the subsamples if examined individually. Comparisons of the 100 iterations for subsample sizes of 200 and above showed all the replicate distributions to be in close agreement. Below a subsample size of 100, however, individual replicates differed greatly due to particular random divergences. Clearly, individual sample sizes of 62, 72, 82, or even 106, as used by Davies (1989, fig 2), are too small to apply length–frequency analysis due to the jagged nature of the few data which masks any emergent pattern.

Orconectes virilis at ELA exhibit both the lowest somatic growth rates and lowest population mortality rates recorded for this species (France 1983). Both of these variables influence the sample size required to successfully apply size–frequency analysis. Higher population mortality rates cause greater inequalities among the proportions of age-classes, necessitating smaller standard deviations between modes, which can be obtained through increased sample sizes (Grant et al. 1987). Conversely, higher growth rates produce increased intermodal distances and thereby reduce the sample sizes needed to discriminate age-classes.

Substrate Type

Physical characteristics of the littoral substrate are known to structure crayfish populations. Size–frequency distributions are shaped by such substrate-regulated phenomena as individual rate of growth (Flint and Goldman 1977), cohort recruitment success (Momot and Gowing 1983), and size-selective predation (Stein 1977). Because of this, France (1985) stated that "extreme care [should be] taken to ensure that the collection sites chosen. . .[are] of uniform physical characteristics. . .i.e. Capelli's (1975) 'type-A substrate' (mostly rocks, boulders and gravel with high shelter potential)." For example, simultaneous collection of *O. virilis* from substrates of sand and rocks at ELA can yield remarkably dissimilar size–frequency distributions (Fig. 7). Adults predominate in the sandy areas whereas a much more representative sample of all sizes was obtained from areas of rocks and boulders. Crayfish size–frequency distributions will vary along a habitat spectrum in relation to the proportion of rocks or sand present in each area (Skurdal et al. 1988). Attempts to derive modal ages through combining such data (e.g. Davies 1989) will consequently be unsuccessful. Interlake comparisons of growth dynamics should therefore be made from crayfish restricted to rock–boulder hab-

TABLE 1. Summary of mean carapace lengths and standard deviations (standard errors of estimates) of best fits to randomly resampled size distributions shown in Fig. 5. Results shown are from the first of three runs with different starting values.

	Means				Standard deviations					
n	μ_1	μ_2	μ_3	μ_4	σ_1	σ_2	σ_3	σ_4	df	χ^2
25	20.99				2.898				13	3.134
	(0.5987)				(0.4663)					
50	20.77				3.532				17	3.540
	(0.5095)				(0.4442)					
75	20.9				3.796				23	9.834
	(0.4393)				(0.3389)					
100	12.35	19.64	25.21		1.128	2.218	2.302		22	2.915
	(0.7646)	(0.9275)	(3.024)		(0.861)	(0.7438)	(1.459)			
200	12.3	19.71	24.65	28.71	1.126	1.942	0.954	1.487	28	1.888
	(0.3407)	(0.244)	(0.3079)	(0.7332)	(0.2981)	(0.2224)	(0.3178)	(0.5885)		
300	12.5	19.69	24.62	28.74	1.228	1.9	1.038	1.343	30	3.234
	(0.3207)	(0.2069)	(0.2674)	(0.5643)	(0.2603)	(0.1905)	(0.2761)	(0.4434)		
400	12.47	19.68	24.6	28.75	1.14	1.862	1.061	1.434	32	3.467
	(0.2443)	(0.1771)	(0.2402)	(0.5073)	(0.1975)	(0.1575)	(0.2519)	(0.3573)		
500	12.35	19.66	24.62	28.82	1.164	1.878	1.046	1.392	32	5.348
	(0.2219)	(0.156)	(0.2029)	(0.4105)	(0.182)	(0.1392)	(0.2093)	(0.297)		

TABLE 2. Summary of proportions (standard errors of estimates) of four components fitted to randomly resampled distributions in datasets with sample sizes from 200 to 500 shown in Table 1. Results are from the first of three runs with different starting values.

	Proportions					
n	π_1	π_2	π_3	π_4	df	χ^2
200	0.07996	0.6792	0.1607	0.08016	28	1.888
	(0.02045)	(0.04946)	(0.05153)	(0.02802)		
300	0.07938	0.6726	0.1789	0.0691	30	3.234
	(0.01704)	(0.0439)	(0.04499)	(0.02083)		
400	0.07945	0.6614	0.1786	0.0806	32	3.467
	(0.0144)	(0.03722)	(0.03978)	(0.02018)		
500	0.07908	0.6617	0.1802	0.07906	32	5.348
	(0.01276)	(0.03234)	(0.03351)	(0.01666)		

itats rather than on entire lake-magnified, and therefore, lake-approximated, values for entire populations.

Sampling Methods

Minnow traps, although useful for both relative (R. France, unpubl. data) and more precise (Momot 1967) estimates of crayfish population size, are often inadequate as a sampling tool for accurately reflecting age composition. This is especially true for populations characterized by low growth rates in which the majority of crayfish are smaller than 24 mm carapace length (W. Momot, Department of Biology, Lakehead University, Thunder Bay, Ont., Canada, pers. comm.; Capelli 1975). Because traps exert a considerable bias in such situations with the capture of predominantly large adult males (Fig. 8; see also Threinen 1958), attempts to discriminate year-classes with traditional graphical probit techniques based on trapping data have proven unsuccessful due to truncated size distributions (e.g. Brewis and Bowler 1982; Somers 1987). Because the proportional representation of the different modes is critical for the accurate estimation of mortality rates, combining trap and SCUBA data may mask such patterns and therefore make impossible the ability to undertake consistent unbiased comparisons among different populations.

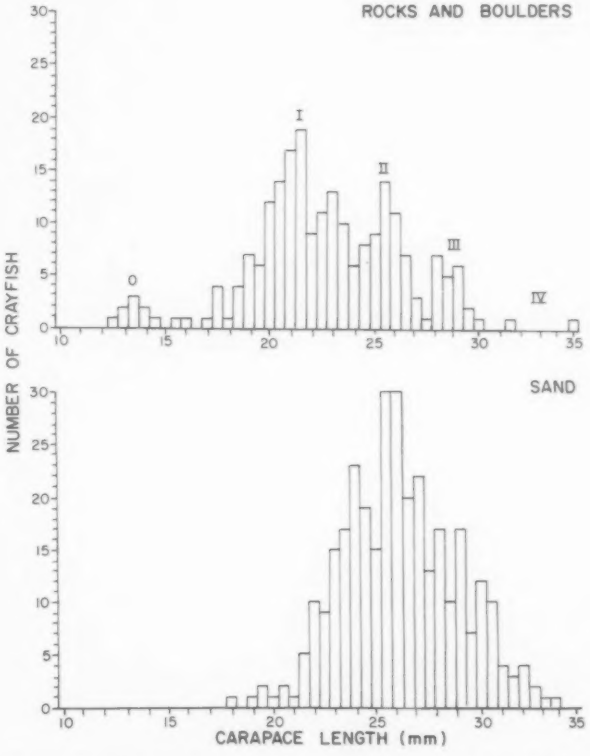

FIG. 7. Comparison of length–frequency distributions of *O. virilis* collected over areas of sand and rock substratum. Sampling was during August 1980 in Lake 239. Positioning of roman numerals in this and in subsequent figures represents age-group mean sizes as calculated by the probit plot method of Cassie (1954).

Species Longevity

Because of variations in molt increment and frequency with time among individuals (e.g. Bowler and Brown 1977; Hazlett and Rittschof 1985), the ability to distinguish successive cray-

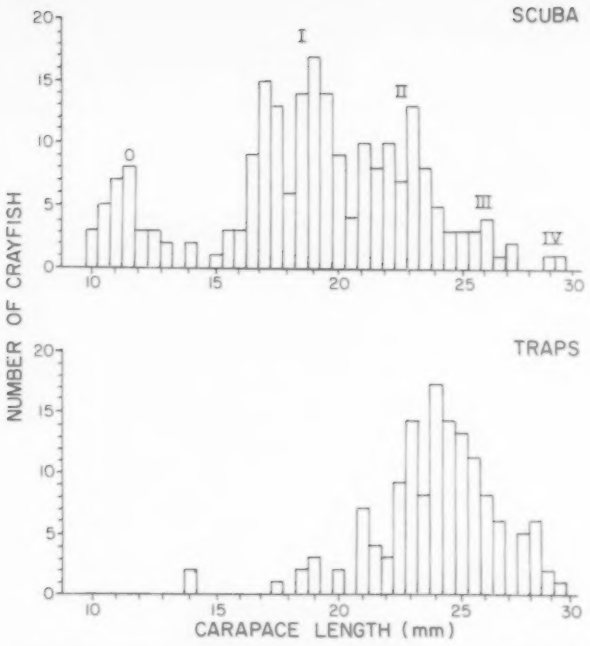

FIG. 8. Comparison of length–frequency distributions of *O. virilis* sampled with SCUBA diving and trapping techniques. Collections were during August 1980 in Lake 224.

TABLE 3. Summary of crayfish sample sizes and separation of age-classes assuming that four age-classes are present in each sample. Separation is expressed as the difference in adjacent mean lengths divided by the mean of group standard deviations. Data were analyzed using Macdonald and Pitcher's (1979) method.

			Separation			
Lake	Date	*n*	0–I	I–II	II–III	III–IV
223	Aug. 79	132	6.9	3.2	3.0	
223	June 80	275		5.0	2.8	2.6
223	July 80	240		4.0	3.4	4.5
223	Sept. 80	291	4.8	3.6	4.4	
224	Oct. 79	224	5.6	3.0	2.5	
224	Aug. 80	220	5.4	3.3	2.9	
239	Sept. 79	221	5.5	3.1	3.9	
239	Aug. 80	234	5.9	3.4	4.0	
240	Oct. 79	282	4.3	3.4	1.9	
240	Oct. 80	239	4.8	3.5	3.7	

fish year-classes can become increasingly problematic. For long-lived species, overlap of sizes from neighboring age-classes due to consistently higher growth rates (e.g. Flint 1975) or, alternatively, persistent stunting (e.g. Svardson 1949) will restrict use of length–frequency data to identifying only the first two or three modes (Brewis and Bowler 1982; Pratten 1980). The utility of such indirect estimates of growth is therefore most valid for those species in which the first three year-classes comprise over 90% of the total population at any time (Hopkins 1966, 1967; St. John 1976; Jones 1981; France 1985).

Conclusions

Grant et al. (1987) and Grant (1989) have shown that separations between mean sizes of consecutive age-classes of 2.5 to 3 times the component SD's are required for best results. This requirement is adequately met in the present case with *O. virilis* from ELA (Table 3). Therefore, it is only when the modes meet this quantitative criterion for the degree of their separation that size–frequency data can be used for aging. Provided the four operational caveats are imposed, this vital mathematical constraint is satisfied, and the serial decomposition of mixed frequency distributions into their constituent modal size(age)classes by either graphical or mathematical procedures can be accomplished (e.g. Fig. 9).

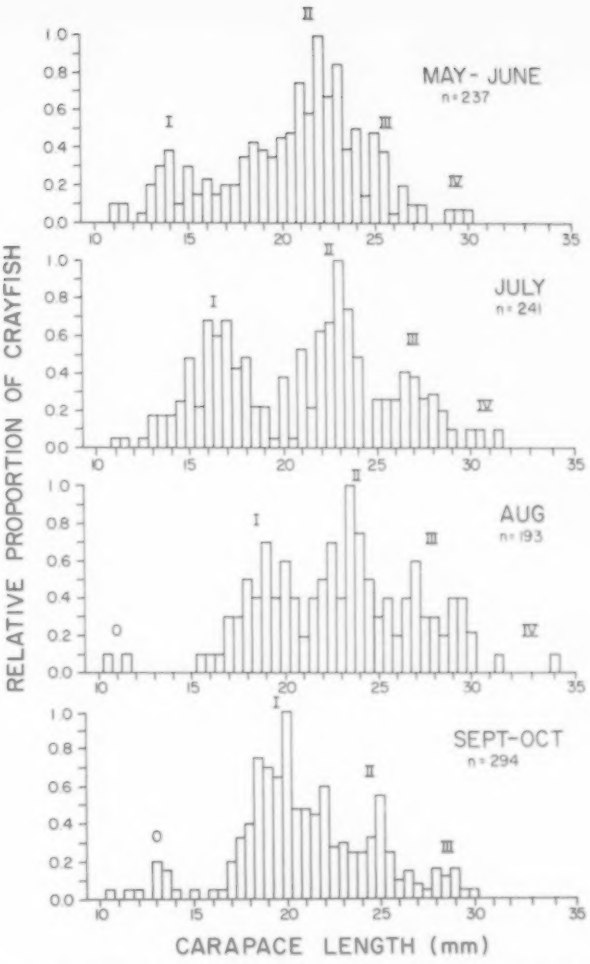

FIG. 9. Length–frequency distributions of crayfish collected with SCUBA over rock substrate in Lake 223 during summer 1979. Refer to France (1985, fig. 1) for progression of calculated mean sizes ± fiducial limits with time.

Obviously, the extent of overlap in size between different age-classes will dictate the relative success of size–frequency analysis. The ability to achieve an appropriate criterion based on modal separation will be hindered through use of data collected with traps or from nonrock substrates or for those species with longevities exceeding 4 yr. In such cases the sample sizes necessary to distinguish modes will increase (see simulations in Grant et al. 1987) above the present suggested value of 200. Separation of sexes in an effort to obtain more precise demo-

graphic estimates would necessitate increases in sampling effort to levels which may be logistically difficult to regularly achieve.

Together, the three validation checks for the particular example of *O. virilis* in ELA lakes confirm rather than refute indirect aging methods and substantiate Flint's (1975) claim that "growth obtained from the statistical analysis of population frequency distributions, an often maligned technique in population biology, can truly represent the growth pattern of crayfish."

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Fecundity, Atresia, and Egg Size of Captive Atlantic Cod (*Gadus morhua*) in Relation to Proximate Body Composition

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Captive Atlantic cod (*Gadus morhua*) were fed at four ration levels (starvation, maintenance, moderate, and excess) for periods of 6–9 mo prior to and during spawning. At the end of the experiment, water, protein, glycogen, and fat contents of the liver, white muscle, and ovary were estimated. The depletion of the white muscle and liver was related to oocyte maturation and in particular to the proportion of eggs spawned (PES). The influx of protein into the ovary, the mean hydrated egg diameter, and the egg dry weight all reached maximum values at 10% PES and subsequently declined. Mean vitellogenic oocyte diameter was small prior to spawning but rose to a maximum at PES = 10%. Cod with high condition factors produced more previtellogenic oocytes and used a larger fraction during vitellogenesis. Actual fecundity of specimens deprived of food during the spawning period was between 20 and 80% of the potential fecundity depending on the nutritional status of the fish. Intensity of atresia in moderate ration fish increased from 0% at PES = 0% to 33% at PES = 80%. Estimates of durations of α-atretic vitellogenic oocytes varied between 10 and 13 d at 8°C assuming a spawning period of 50 d.

Des morues de l'Atlantique (*Gadus morhua*) en captivité ont été soumises à quatre régimes alimentaires différents (alimentation insuffisante, minimale, moyenne ou excessive) pendant 6 à 9 mo, avant et au cours de la période de frai. Les teneurs en eau, protéines, glycogène et lipides du foie, des muscles blancs et des ovaires ont été déterminées à la fin de l'expérience. Les pertes observées dans les muscles blancs et le foie ont été liées à la maturation des oocytes et, en particulier, à la proportion d'oeufs pondus (POP). L'arrivée de protéines dans l'ovaire, le diamètre moyen des oeufs hydratés et le poids sec des oeufs ont atteint leur valeur maximale à une POP de 10 % et ont décliné par la suite. Le diamètre moyen des oeufs vitellogènes, petit avant le frai, a été maximal pour une POP de 10 %. Les morues ayant des coefficients de condition élevés ont produit plus d'oeufs prévitellogènes et en ont utilisés une plus grande partie durant la vitellogenèse. La fertilité réelle des spécimens soumis à une alimentation insuffisante en période de frai a représenté 20 à 80 % de la fertilité possible selon l'état nutritionnel des poissons. Le pourcentage d'atrésie chez les poissons soumis à une alimentation moyenne est passé de 0 % (POP de 0 %) à 33 % (POP de 80 %). Les valeurs approximatives de la durée des oocytes vitellogènes α-atrétiques ont varié de 10 à 13 jours à 8° C en supposant une période de frai de 50 jours.

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Atlantic cod (*Gadus morhua*) are determinate spawners; in other words, the potential fecundity defined as the standing stock of advanced or vitellogenic oocytes present prior to spawning is equivalent to the number of eggs spawned. There is no evidence for de novo vitellogenesis during spawning (West 1970; Kjesbu et al. 1990; cf. also the description of "group synchronous" ovaries in Wallace et al. 1988) although a proportion of the oocytes included in the potential fecundity estimate may become atretic. There have been no reports to date of any substantial interannual variation in fecundity (Oosthuizen and Daan 1974; Kjesbu 1988).

Cod have a high potential fecundity which sustains many batches of eggs over a long spawning period (Kjesbu 1989), and the size of vitellogenic oocytes remains small prior to spawning but rises sharply prior to hydration (Kjesbu et al. 1990). Thus, a large number of small vitellogenic oocytes constituting the annual fecundity are produced at a relatively low energetic cost. Under favourable conditions, which include ample body reserves and a plentiful food supply, the more energy-expensive process of increasing egg size can be regulated to maximum advantage. Yolk consists of 20% fat and 80% protein (Plack et al. 1971) which is probably mobilised from the liver and white or fast myotomal muscle (Love 1980), respectively. The mean egg diameter of the first batch of eggs and fish length have been shown to be significantly positively correlated in captive cod with a common experimental history

(Kjesbu 1989). In addition the mean egg diameter decreased in successive batches as the spawning period progressed in the same way as observed for haddock (*Melanogrammus aeglefinus*) (Hislop et al. 1978).

The present work is designed to study the regulation of fecundity by analysing the egg production of fish of differing nutritional status. The number of previtellogenic oocytes, egg diameter, and egg dry weight are measured and the potential fecundity prior to spawning is compared with the actual fecundity. The difference which comprises the losses through atresia is calculated by measuring the intensity of atresia and estimating the duration of the atretic stage. These results are in turn related to changes in the composition of the white muscle, liver, and ovary.

Materials and Methods

Experimental Design

The experiment was designed to produce female Atlantic cod of differing nutritional status by varying the food intake. The following four feeding groups were established for periods of 6 or 9 mo (see below) using reared coastal cod from the Austevoll Aquaculture Research Station, N-5392 Storebø, Norway: starvation, maintenance ration (i.e. constant body weight), moderate ration (≈0.5% wet body weight·d^{-1}), and excess ration (fed to satiation). The maintenance ration group was established in May to include the postspawning period (i.e. fish with depleted body reserves), while the other groups of fish were fed to satiation during the summer to restore their body reserves after spawning and then put on their respective rations in August to be in advance of vitellogenesis which begins between September and November (Kjesbu 1991). Recovered fish were in good condition after spawning, indicating that starvation would need to be severe to elicit any significant effect on fecundity. As age is not directly correlated with fecundity in cod (Oosthuizen and Daan 1974), fish were selected by length.

In January, several fish in each of the four groups had commenced spawning as shown by a high concentration of eggs in the tank water. Most females were then killed and analysed as described below. Representatives of each group classified by ovarian biopsy (Kjesbu 1991) and morphology of the vent (Morrison 1990) as prespawners were placed in indoor spawning chambers of 20 m^3 of seawater in order to count the total number of eggs spawned (designated actual fecundity) and to estimate the total egg dry weight (cf. Kjesbu 1989). Because of signs of aggression among males (Kjesbu 1989), only a single male (from the moderate ration group) was kept with each female. Special attention was directed towards quantitative sampling of the eggs. Females that spawned just after placement in the chambers were consequently replaced. The eggs were collected on an outlet sieve at the surface and by a hand-held net. Some eggs from each batch settled out on the bottom of the chamber, and a correction was made to the original estimate of the number of eggs in the batch based on the following: (1) the sinking rate of the eggs while kept in a beaker, (2) the fertilization rate (being inversely related to the number of eggs settling out), (3) the amount of eggs collected near the bottom using the hand-held net, and (4) the shape of the curve relating batch size and batch number expecting a smooth dome-shaped curve (Kjesbu 1989). If points 1–3 showed settling of eggs, and the curve was discontinuous at that particular batch number, the number of eggs that had dropped to the bottom was found by interpolation using this curve. Consequently, the actual fecundity included both the eggs collected in midwater and eggs found to have settled on the bottom; the latter (i.e. number of eggs settled per number of eggs collected) was generally low (mean 4%, range 0–15%).

Three of the spawning females used in a previous experiment (Kjesbu 1989) were also kept throughout the whole spawning period but subsequently killed. The characterization of the spent ovaries and the data relating to actual fecundity and total egg dry weight were included in the present study. These fish were held under similar conditions to the moderate ration fish and lost 5–12% of their egg production which settled out on the bottom.

Fish Husbandry

Fish that formed the maintenance ration group ($n = 31$) were brought to the laboratory in September of the year prior to the experiment. At the start of the experiment in August, a further 71 fish were brought to the laboratory and randomly divided to form the starvation and moderate ration groups. The maintenance and moderate ration groups were kept together in an outdoor 30-m^3 seawater tank but were kept apart by a net. The starvation group was kept in another 30-m^3 tank. A gonad biopsy in December showed that the starvation group comprised 19 females and 22 males, while the moderate ration group comprised 17 females and 13 males. During the autumn, six specimens on maintenance ration were removed because of skin infections. Excluding this number of diseased fish, the maintenance ration group included 11 females and 14 males. The excess ration group comprised a large number of extremely well-fed fish (≈3000 specimens) that were kept in a sea cage (720 m^3) at the Austevoll Aquaculture Research Station. In January, a sample was taken from this cage and the specimens sexed with the aid of an ultrasonic apparatus (Scanner 450, Pie Medical); 25 females were selected by length (to fit the length distributions of the other ration groups) and subsequently transported to the laboratory. They were temporarily kept together with the moderate ration group. All fish used were individually marked (Lea tag). In January the starved and moderate ration fish were 4 yr old, while those on maintenance ration and excess ration were 3–5 and 3, respectively. All fish were repeat spawners, as reared cod spawn at the age of 2, some males even at the age of 1 (T. H. Riple, Austevoll Aquaculture Research Station, N-5392 Storebø, Norway, pers. comm.).

Feeding and Physical Parameters

Feeding studies on cod have almost exclusively been concentrated on smaller specimens (Jobling 1988). Wild cod older than 2 yr typically show a specific growth rate (G) defined as

$$G = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \cdot 100$$

(W = whole body weight (grams); t = time (days)) of about 0.2 between May and November, the main growth period (Jørgensen 1989). Our moderate ration fish should ideally grow at the same rate. Because of the lack of data on daily food consumption the interest in food shown by the fish was used as a measure of the amount of food needed; the moderate ration fish were fed until interest in the food started to drop, feeding frequency being three, occasionally two, times per week. The

study by Lied et al. (1985) suggests a maintenance ratio of 25% of satiation. The maintenance ration was initially set to be 30% of the moderate ration, as the latter was appraised to be somewhat below satiation. Excess ration fish were fed to satiation five times per week.

To monitor the growth of the fish, whole wet body weight (W) (to the nearest 10 g) and total length (L) (to the nearest 1 cm) were recorded monthly from August to January. The excess ration fish were measured only in January. Prior to measurement the fish were deprived of food for 2–5 d followed by exposure to anaesthetic (50 ppm benzocaine) dissolved in oxygenated seawater. The data on individual body weights were used to calculate the daily ration for the next 4 wk, the purpose being to produce fish of differing nutritional status using Fulton's condition factor (K):

$$K = \frac{W}{L^3} \cdot 100.$$

The moderate ration was calculated from information aquired during the first 4 wk and corresponded to a maximum of 0.5% wet body weight·d^{-1}. Fish on the maintenance ration became more and more voracious during the autumn. This, together with the observation that the larger fish moved too slowly to feed effectively, indicated that it was necessary to increase the ration size and each time give this in one lot to the fish to reduce competition for food. When feeding was terminated on 9 January, excess ration and moderate ration fish showed little appetite, while some fish on the maintenance ration were still hungy.

Wet pellets from the Austevoll Aquaculture Research Station were used as food. Herring (*Clupea harengus*) and capelin (*Mallotus villosus*) were the main components and the pellets were enriched with vitamins, including C and E, and minerals. The available energy content was 9·0 kJ·g dry matter^{-1} with 62, 25, and 13% from protein, fat, and carbohydrate, respectively (cf. Lie et al. 1988).

Water temperature was recorded weekly throughout the whole feeding period: starved fish experienced a mean temperature of 8.9°C (SD = 0.72), while the moderate and maintenance ration fish experienced 8.5°C (SD = 0.36). (This constant temperature provided by fjord water from 120 m depth made it easier to predict the ration size.) In the same period the temperature (at 2 m depth) for the excess ration fish kept in cages gradually decreased from 16 to 8°C (mean = 11.0, SD = 2.92).

Chemical and Histological Analyses and Oocyte Counting

Fish were killed on 15 January and the body weight and length were recorded as described above. Prespawning and spawning females were differentiated by visual inspection of the ovaries, the first referring if not otherwise stated to specimens with the most advanced oocytes in late true vitellogenesis (stage 4 in Kjesbu 1991) and the latter to specimens with hyaline (hydrated) oocytes or ovulated oocytes (stage 5). The ovary, liver, and remaining viscera were dissected out of the fish and weighed to the nearest gram. Five fish, with length (x) from 58 to 65 cm, were analysed by dissection to give the weight (y) of the head and the vertebral column (grams). The following formula was calculated:

$$(1) \quad y = 42.38 \cdot x - 1627.8 \qquad (r^2 = 0.966, P < 0.01).$$

Samples of white muscle (taken from the point of maximum flexure (Greer Walker 1971)), liver, and ovary were analysed for water content, ash, protein, fat, and glycogen. Water content and ash were determined by conventional methods using 110°C (24 h) and 550°C (to constant weight), respectively. Protein was analysed by the micro-Kjeldahl technique (Crooke and Simpson 1971) and fat was extracted from the liver with ethyl acetate. Fat in the white muscle and ovary was extracted with chloroform–methanol according to Folch et al. (1957). The determination of fat was by gravimetry. Glycogen was analysed by an enzymatic method described by Hemre et al. (1989).

Ovaries for histological studies (light microscopy) were from two sources: (1) the present experiment including 12 ovaries of prespawning fish from different feeding groups and (2) the experiment described in Kjesbu et al. (1990) including two prespawning and eight spawning ovaries of moderate ration fish. In the latter material the portion of the total number of eggs spawned (PES, see below) by each female was known. The ovary samples were fixed in Karnovsky's fluid, dehydrated, embedded in historesin, sectioned (1 μm), and stained with toluidine blue. Normal oocytes and α-atretic vitellogenic oocytes (Hunter and Macewicz 1985) within a grid (approximately 50 mm^2, generally about 300 oocytes) were counted. The result for each specimen was based on only one section (middle of the right ovary lobe), as the ovary of the cod is homogeneous (Kjesbu 1988; Kjesbu et al. 1990). The number of previtellogenic oocytes observed within the grid was divided by the total number of oocytes within the same grid, and, similarly, the number of atretic vitellogenic oocytes in relation to the total number of developing oocytes (normal + atretic) was also determined and designated the intensity of atresia.

An automatic fish egg counter (Witthames and Greer Walker 1987) was used to determine the number and size of the vitellogenic oocytes in the ovary (n = 62); a single sample (≈10 g) was examined from each fish. The preparation of the samples for this apparatus included 6 mo of digestion in Gilson's fluid (to break down the connective tissue, thus liberating the oocytes), storage in 2% formaldehyde, and cleaning procedures (cf. Witthames and Greer Walker 1987; Kjesbu et al. 1990). Just prior to examination in the fish egg counter, each sample was studied under a Micro Fisch viewer (Zeiss) to assess the amount and size of debris and the range in oocyte diameter. These data were taken into account when interpreting the result. The aforementioned differentiation of the ovaries into prespawning and spawning states was finally checked with reference to the size frequency distribution of the oocytes (Kjesbu et al. 1990). The number of vitellogenic oocytes in the prespawning ovary was designated the potential fecundity.

Chemical Composition

It was assumed that the chemistry of the fish was correlated with the number of batches spawned at sampling. A method recently developed (Kjesbu et al. 1990) makes it possible to calculate this parameter or more correctly the portion of the total number of eggs spawned per season (PES) by considering the number of vitellogenic oocytes per gram wet ovary (NG). NG has been shown to be significantly reduced as PES increases. The NG results from the fish egg counter were consequently used to give the PES values for the specimens killed on 15 January.

In several instances the results were standardized to a 60-cm fish (a typical total length) based on linear regressions. If the parameter in question (y-axis) was not significantly related to length (x-axis), the mean y was used instead (stated in text).

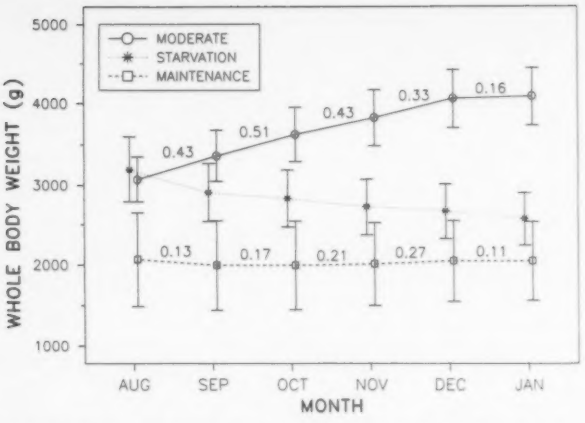

FIG. 1. Change in the whole body weight of starved fish and maintenance and moderate ration fish during the feeding period. The mean weight and 95% confidence interval are given. The same specimens were weighed each month. Numbers give the daily ration size relative to the whole body weight (on a wet weight basis).

Each feeding group was studied separately. The Fulton's condition factors recorded on 15 January were used to calculate standard wet body weights. Data on the gonosomatic index (GSI), defined as

$$\text{GSI} = (\text{gonad wet weight/whole wet body weight}) \cdot 100,$$

and the hepatosomatic index (HSI), defined as

$$\text{HSI} = (\text{liver wet weight/whole wet body weight}) \cdot 100,$$

were used to calculate the standard ovary and liver weights, respectively. The weight of the head and vertebral column was found from equation (1) above. The weight of the viscera was set at 100 g, a representative value even for the starved 60-cm fish. The weight of the red and white muscle was then calculated.

The change in the proximate body composition during spawning of a standard female was studied in two different ways, designated Approach 1 and Approach 2. In Approach 1 the chemical data from spawning fish were averaged irrespective of the portion of the total number of eggs spawned (PES) by each specimen (i.e. simply comparing prespawning and spawning fish), while in Approach 2 the chemical composition of a fish was studied in relation to its particular PES value (i.e. a much more detailed approach) focusing on the more numerous starved females (see below). Kjesbu et al. (1990) used fish on a moderate ration when establishing the relationship between PES and NG. Therefore, there was a possibility that the derived formulae were not appropriate for starved fish. The NG method demanded (1) that starved fish showed the same packing density of the oocytes at a given PES as fish on moderate ration and (2) that these particular females also started spawning at a NG of about 6000. To test the first assumption, the NG of prespawning females (i.e. PES = 0) from all four groups were tested versus the corresponding mean vitellogenic oocyte diameter. Starved females and females on excess and moderate ration did not show significantly different slopes or intercepts (ANCOVA, $0.10 < P < 0.25$) and the few fish on maintenance ration did not differ in this respect either. Concerning the second assumption, the lowest NG value observed for the

TABLE 1. Proximate composition (% wet weight, mean values) of prespawning and spawning fish in relation to their nutritional status. Excess and moderate ration groups showed similar chemical values and are therefore combined. Atresia occurred in fish with low condition factors that were fed the maintenance ration. All fish were sampled at the same time (15 January). Chemical parameters included in further studies (see text) are given with the coefficient of variation ((standard deviation/mean)·100) in parentheses. n = number of fish examined.

Ration group	n	White muscle					Liver					Ovary				
		Water	Protein	Glycogen	Fat	Ash	Water	Protein	Glycogen	Fat	Ash	Water	Protein	Glycogen	Fat	Ash
Prespawning fish																
Excess and moderate	4	79.0	18.6 (3.6)	0.4	0.4	1.3	37.7	4.8	6.4	49.4 (6.3)	0.6	71.5	22.4 (2.6)	0.2	4.6 (6.9)	1.5
Maintenance	3	80.0	16.9 (1.8)	0.2	0.4	1.2	37.1	4.7	5.3	51.6 (8.3)	0.7	72.7	20.4 (10.8)	0.1	4.2 (21.8)	1.7
Starvation	5	83.1	15.3 (8.4)	0.2	0.4	1.2	35.0	4.8	1.3	57.8 (10.3)	0.5	74.1	20.5 (8.4)	0.1	3.7 (13.4)	1.5
Atresia (%)																
10	1	85.1	13.7	0.2	0.4	1.1	27.7	9.0	0.4	59.3	0.6	78.0	18.0	0.2	2.7	1.7
100	1	90.8	7.7	0.1	0.5	1.1	76.3	12.0	0.5	7.1	1.2	85.8	11.1	0.2	0.8	1.5
Spawning fish																
Excess and moderate	3	80.6	17.1 (3.0)	0.3	0.4	1.2	39.8	5.7	5.6	46.5 (11.8)	0.8	72.9	21.2 (17.1)	0.2	4.5 (21.4)	1.4
Starvation	8	84.1	13.5 (8.8)	0.2	0.4	1.1	38.2	4.4	0.9	55.1 (17.9)	0.6	74.1	20.8 (8.6)	0.1	3.9 (11.8)	1.3

NOTE: Atresia refers to the number of α-atretic vitellogenic oocytes in relation to the total number of developing oocytes in the ovary. In the fish that showed complete resorption of vitellogenic oocytes the smaller previtellogenic oocytes were also resorbed.

TABLE 2. Change (Δ) in the amount of protein and fat in different organs of a standard female cod (60 cm) during the transition from a prespawning (P) to a spawning (S) condition. n = number of fish used in the calculation; K = Fulton's condition factor (whole wet body weight/total length^3)·100; GSI = gonosomatic index (gonad wet weight/whole wet body weight)·100; HSI = hepatosomatic index (liver wet weight/whole wet body weight)·100; Δ = S − P.

Ration group	n		K		GSI (%)		HSI (%)		Protein (g)						Fat (g)			
									White muscle		Liver		Ovary		Liver		Ovary	
	P	S	P	S	P	S	P	S	P	Δ	P	Δ	P	Δ	P	Δ	P	Δ
Excess	10	10	1.78	1.77	14.9	19.9	12.8	11.6	328	−54	24	2	128	33	243	−37	26	8
Moderate	9	5	1.42	1.31	14.0	18.6	9.8	8.3	246	−66	14	−1	96	16	148	−39	20	4
Maintenance	4	2	1.03	1.09	10.1	12.6	8.9	5.5	133	—	9	—	46	—	102	—	9	—
Starvation	6	10	1.08	1.13	8.1	14.3	6.8	6.1	148	−23	8	−1	39	34	92	−10	7	7
Atresia (%)																		
10	1	—	0.74	—	5.1	—	3.9	—	60	—	6	—	15	—	37	—	2	—
100	1	—	0.67	—	2.4	—	0.9	—	30	—	2	—	4	—	1	—	≈0	—

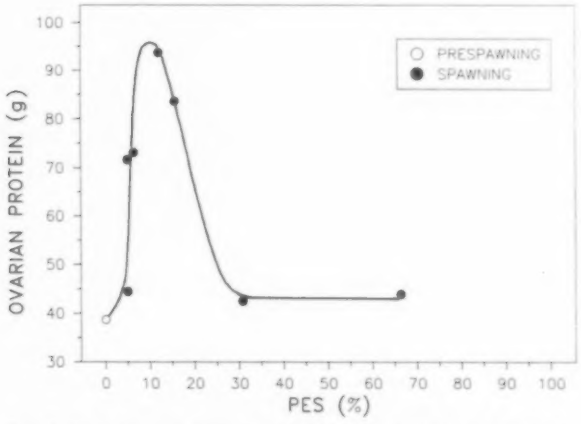

FIG. 2. Variation in the amount of ovarian protein during the spawning period for a standard 60-cm starved specimen. PES refers to the portion of the total number of eggs spawned. The point at PES = 0 is a mean value, while the other points are based on individual fish. The line was drawn by eye.

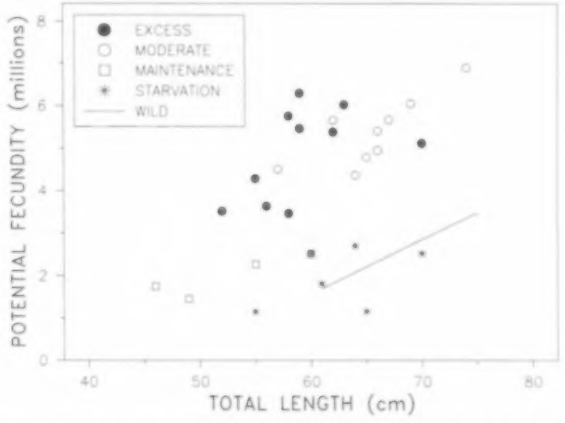

FIG. 3. Relationship of potential fecundity (number of vitellogenic oocytes in ovary prior to spawning) to fish length for specimens kept on different feeding rations and wild fish. The regression line was based on data from Botros (1962).

prespawning starved females was 8700, while the highest number for the spawning starved ones was 5770. It was concluded that the NG method could be used on starved fish. One spawning starved female showed too much debris in the ovarian sample to give a reliable PES value and was excluded.

Results

Growth

Between August and December (125 d), females on the moderate ration changed their body weight by an average of 32.7% (corresponding to a specific growth rate (G) of 0.224) and the starved and maintenance ration groups by −16.8 and 0.7%, respectively (Fig. 1). Many females, irrespective of length, had commenced spawning on 15 January: 53% in the starvation group, 40% in the maintenance group, 35% in the moderate group, and 44% in the excess group. In January the length range of the females in the four feeding groups was 51–77 cm in the starvation group, 46–74 cm in the maintenance group, 57–76 cm in the moderate group, and 52–70 cm in the excess group.

The starved females did not increase in length and lost body weight most rapidly during the first 4 wk (Fig. 1); from September onwards the loss was stable at 2.7 g·d^{-1}. Starved cod swam less than the other groups, typically staying on the bottom or gliding through the water. Based on the food consumption, the metabolism of the maintenance ration fish approximately doubled during the autumn, from 11.4 to 24.0 J·g fish^{-1}·d^{-1}. Females on moderate ration showed a feed conversion (grams dry feed per gram fish wet weight gain) of 1.09.

The splitting of the sample brought to the laboratory in August (i.e. at the start of the experiment) was random, but nevertheless those females designated starved showed a significant negative correlation ($R = -0.687$, $0.001 < P < 0.01$) between total fish length (L) and Fulton's condition factor (K), while those designated moderate did not ($r = -0.173$, $P \approx 0.50$). The K in the two groups was, however, not significantly different ($0.05 < P < 0.10$, Wilcoxon's two-sample test). The whole sample showed a significant negative correlation between K and L ($r = -0.569$, $P < 0.001$). These data were compared, using ANCOVA, with those for females on the maintenance ration; the intercepts were significantly different ($P < 0.001$) but not the slopes ($0.50 < P < 0.75$).

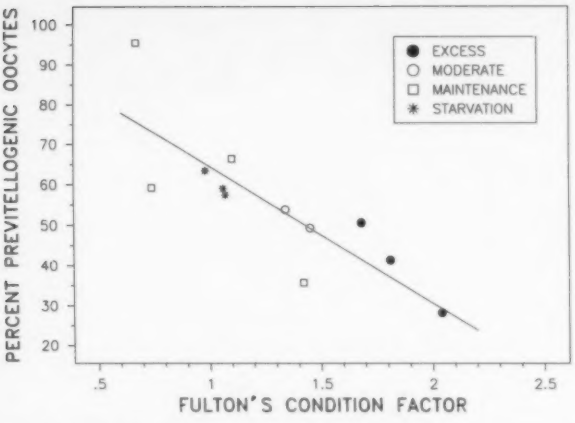

FIG. 4. Number of previtellogenic oocytes per total number of oocytes in ovary prior to spawning in relation to Fulton's condition factor.

At the start of the experiment the K of a standard female with a length of 60 cm was 1.33 in the starvation group, 1.08 in the maintenance ration group, and 1.19 (mean value) in the moderate ration group. In December, based on new regressions, the K had changed to 1.10, 1.05, and 1.40 (mean value), respectively. The weight gain and weight loss of the moderate and starved fish, respectively, were not significantly correlated with the length of the fish ($P > 0.10$). There were, however, trends in the data within each group indicating that the smaller starved fish lost relatively more weight and that the larger moderate ration fish gained relatively less weight. In the case of the maintenance ration fish, however, the regression coefficient (slope) was significantly negative ($0.02 < P < 0.05$); the smallest females gained about 10% in weight, while the largest lost about 10%.

Chemical Composition of Prespawning and Spawning Fish

Chemical data from excess and moderate ration females were combined, as there were apparently no differences (Table 1). None of the spawning maintenance ration females were analysed. Two of the prespawning specimens in the maintenance ration group were separated in the table because of the extreme values. These two specimens and one starved prespawning female showed atresia (see below) of between 3 and 100%; this was coincidental with a low protein content (<14.5%) in white muscle. The fish with the lowest protein content did not produce vitellogenic oocytes at all. The oocytes were arrested/resorbed at the cortical alveoli stage (for description of stages, see Kjesbu and Kryvi 1989) and there was further evidence of resorption of previtellogenic oocytes.

Approach 1

Egg dry weight of wild cod consists of 73–77% protein and 10–12% fat (Lønning et al. 1988); similarly, the present ovaries showed 75–82% protein and 6–16% fat on a dry weight basis. The protein was assumed to be mobilised from the white muscle rather than the red muscle (Greer Walker 1971; Love 1980) and the fat from the liver (Table 1). Multiplications of the standard organ weights with the actual mean chemical values (Table 1) were used to obtain the results in Table 2. The protein content in white muscle was probably overestimated by about 5%, as the red muscle content of the myotome (Greer Walker and Pull 1975) was not subtracted; however, this should not affect the calculated change. There are, however, reasons (Greer Walker 1971) to believe that the ratio of red muscle to white muscle was higher in the spawning fish, especially in the starved ones, implying that the change could in reality be larger.

Approach 2

The change in the amount of protein in the ovary in relation to PES is illustrated in Fig. 2. Fat and protein contents were highly correlated ($r = 0.975$, $P << 0.01$), the ratio being from 17.9 to 19.6%. The amount of fat in the liver using the same specimens as those used in Fig. 2 became significantly reduced ($0.01 < P < 0.02$) as PES increased. Such a detailed picture could not be shown ($P > 0.50$) for muscle protein because of the problems of assessing white muscle mass.

Potential and Actual Fecundity

Potential fecundity (i.e. the number of vitellogenic oocytes in prespawning fish ($n = 29$)) was significantly linearly related to total length ($r^2 = 0.245$, $0.001 < P < 0.01$; Fig. 3) and whole body weight ($r^2 = 0.801$, $P < 0.001$). All fish included were killed on 15 January and showed a Fulton's condition factor of 0.83–2.04 (see use of the equation below), a much bigger range than normally observed for wild fish (Kjesbu 1988). Consequently, the adding of both length and weight as independent variables improved the regression significantly ($0.001 < P < 0.005$, Fisher test) compared with the regression which had whole body weight as the only variable. The following relationship was established between the potential fecundity (F, millions) and the whole wet body weight (W, grams) and total length (L, centimetres):

$$(2)\quad F = 1.983 \times 10^{-3} \cdot W - 9.922 \times 10^{-2} \cdot L + 3.562 \qquad (R^2 = 0.862,\ P < 0.01).$$

The relative standardized strength (i.e the b-primes) of W and L on the estimate of F was 1.167 and -0.368, respectively; W was approximately three times more important than L. There was no significant difference ($0.10 < P < 0.50$, Kruskal–Wallis test) in the residuals, $((Y - \hat{Y})/Y) \cdot 100(\%)$, between the four feeding groups; equation (2) fitted all groups. A standard 60-cm female, based on the Fulton's condition factor values in Table 2, showed the following potential fecundities (millions): excess ration, 5.25; moderate ration, 3.70; maintenance ration, 2.03; and starvation, 2.25. (A wild cod shows a condition factor of about 1 and, when 60 cm, a potential fecundity of about 1.5 million (Botros 1962).) The reason for the difference in potential fecundity between the experimental groups was examined by relating Fulton's condition factor (K) (x) to the percentage of previtellogenic oocytes (y) (Fig. 4):

$$(3)\quad y = 98.364 - 33.891 \cdot x \qquad (r^2 = 0.697,\ P < 0.001).$$

Minimum (1.03) and maximum (1.78) standard values of K (Table 2) provided estimates of 63.5 and 38.0%, respectively, implying, including the result on standard potential fecundity, a corresponding number of 5.6 and 8.5 million previtellogenic oocytes; fish in better condition produced a higher number of previtellogenic oocytes and utilized a larger fraction during vitellogenesis.

The potential fecundity calculated from equation (2) was compared with the actual fecundity (i.e. the number of eggs actually spawned by a particular female) (Table 3). A macroscopic examination of three spent ovaries (fish 3, 4, and 5

TABLE 3. Data relating to the 11 females observed during the whole spawning period. W = whole wet body weight; L = total length; K = Fulton's condition factor (i.e. $(W/L^3)\cdot 100$); potential fecundity = number of vitellogenic oocytes in ovary prior to spawning (estimated from equation (2)); total egg dry weight = actual fecundity·weighted mean individual egg dry weight; ΔW = ((W (spent) – W (prespawning))/W (prespawning))·100.

Fish		Prespawning			Spawning						
					Mean temp.	Fecundity (millions)		Actual/ potential fecundity	Total egg dry weight	Spent	
Ration	Number	W (g)	L (cm)	K	(°C)	Potential	Actual	(%)	(g)	ΔW (%)	K
Starvation	1	2550	62	1.07	8.6	2.47	1.49	60.3	132	−20.4	0.85
Starvation	2	1580	55	0.95	8.7	1.24	0.60	48.4	58	−34.2	0.63
Maintenance	1	1500	50	1.20	8.7	1.58	0.69	43.7	55	−20.0	0.90
Maintenance	2	3550	74	0.88	8.7	3.26	0.73	22.4	60	−11.3	0.78
Moderate	1	4800	67	1.60	8.9	6.43	2.86	44.5	266	−26.3	1.18
Moderate	2	3750	64	1.43	8.8	4.65	3.22	69.2	275	−34.9	0.93
Moderate	3	2800	56	1.59	5.2	3.56	2.77	77.8	199	−35.0	0.98
Moderate	4	6700	75	1.59	6.2	9.41	5.40	57.4	468	−37.9	0.99
Moderate	5	4200	64	1.60	8.2	5.54	3.94	71.1	359	−35.5	1.03
Excess	1	4580	64	1.75	8.8	6.29	4.10	65.2	353	−50.9	0.86
Excess	2	3520	61	1.55	6.5	4.49	2.24	49.9	222	−38.1	0.96

NOTE: Fishes 3 and 4 (moderate ration) and fish 2 (excess ration) were kept during the spawning in outdoors tanks; the others were kept indoors. The prespawning weight and length data of fishes 3, 4, and 5 (moderate ration) were recorded on 16 December instead of 15 January. This was considered unimportant because the other prespawning moderate ration fish showed no significant change in body weight ($0.40 < P < 0.50$, t-test for paired comparisons) from December to January.

(moderate ration)) showed very few hyaline oocytes left (<100) and also an insignificant number of vitellogenic oocytes. Fish 1 (excess ration) died 6 d after the last spawning. Its ovary, however, contained about 18 000 hyaline oocytes which probably constituted one more batch (there were too few vitellogenic oocytes for more batches); this was taken into consideration. The females spawned between 20% (fish 2 (maintenance)) and 80% (fish 3 (moderate)) of the potential number of vitellogenic oocytes. There was apparently no effect of water temperature on this result. Fulton's condition factor prior to spawning was significantly positively correlated ($r = 0.621$, $0.01 < P < 0.05$) with the ratio of actual to potential fecundity. It should, however, be noted that the same length and weight data were used to calculate both the potential fecundity and the condition factor (see Sokal and Rohlf 1981).

Morphology of Atresia

Atretic vitellogenic oocytes were easily recognisable (the present study considers only the α stage), and a number of different phases were distinguished based on the shape and location of the chorion (zona radiata), proliferation of the follicle cells, and breakdown of the yolk granules (Fig. 5). The central area of the oocyte was less affected by the degenerative process during the early phases of atresia. In later phases, the yolk was resorbed and there were large numbers of different vesicles present in the cytoplasm. Blood vessels were present on the surface of the atretic oocytes at all phases.

Atresia in Spawning Fish

Histological studies showed that the intensity of atresia in moderate ration fish increased with PES (Fig. 6). Many atretic follicles (i.e. later than the α stage described in Fig. 5) were observed at PES = 80. Fish on moderate ration showed an average actual fecundity of 64% of the potential fecundity (Table 3), implying that totally 36% of the developing oocytes were resorbed. Based on Fig. 6, the mean weighted intensity of atresia was 7.2% (based on the figures (100 − PES)·intensity of atresia). Therefore, with a spawning period of 50 d (water temperature 8°C) (Kjesbu 1989), the mean duration of an atretic oocyte should be 10 d. The PES values included in the calculation of the mean weighted intensity of atresia could be biased because present α-atretic oocytes were excluded (digested in the Gilson's fluid) but probably not those appearing later on (Macer 1974). (The PES method refers, as it stands, to the situation in the ovary at the time of sampling). The error (maximum ±3%) in PES, found by including data on the number of vitellogenic oocytes left in the ovary (Kjesbu et al. 1990), produced, however, only an insignificant change in the mean weighted intensity of atresia and consequently in the estimate of the duration of the atretic stage. This calculation assumed no atresia for PES > 80%. Extrapolation of the data in Fig. 6 increased the duration to 13 d. Introduction of a maximum intensity of atresia of 50% (Hunter and Macewicz 1985) gave a duration of 12.5 d.

Egg Size

It has been suggested that egg size is determined during the spawning period (Kjesbu et al. 1990), and in this respect it is of particular interest to note the influx of protein to the ovary at the beginning of spawning (Fig. 2). To further investigate this phenomenon, the total egg dry weight produced per batch, the egg diameter, and the egg dry weight of two starved specimens were plotted versus PES (Fig. 7a–7c; Table 3 gives L and K) where PES was calculated as (cumulative number of eggs shed at a given batch number/actual fecundity)·100. According to Fig. 2 the main influx of protein occurs when PES is between 0 and 30%. The egg diameter and egg dry weight were maximum in the same period, while the total egg dry weight per batch increased up to PES ≈ 50%. The mean vitellogenic oocyte diameter in the spawning ovary of both starved and moderate ration fish is shown in Fig. 7d. In the same period as the main influx of protein took place the vitellogenic oocyte

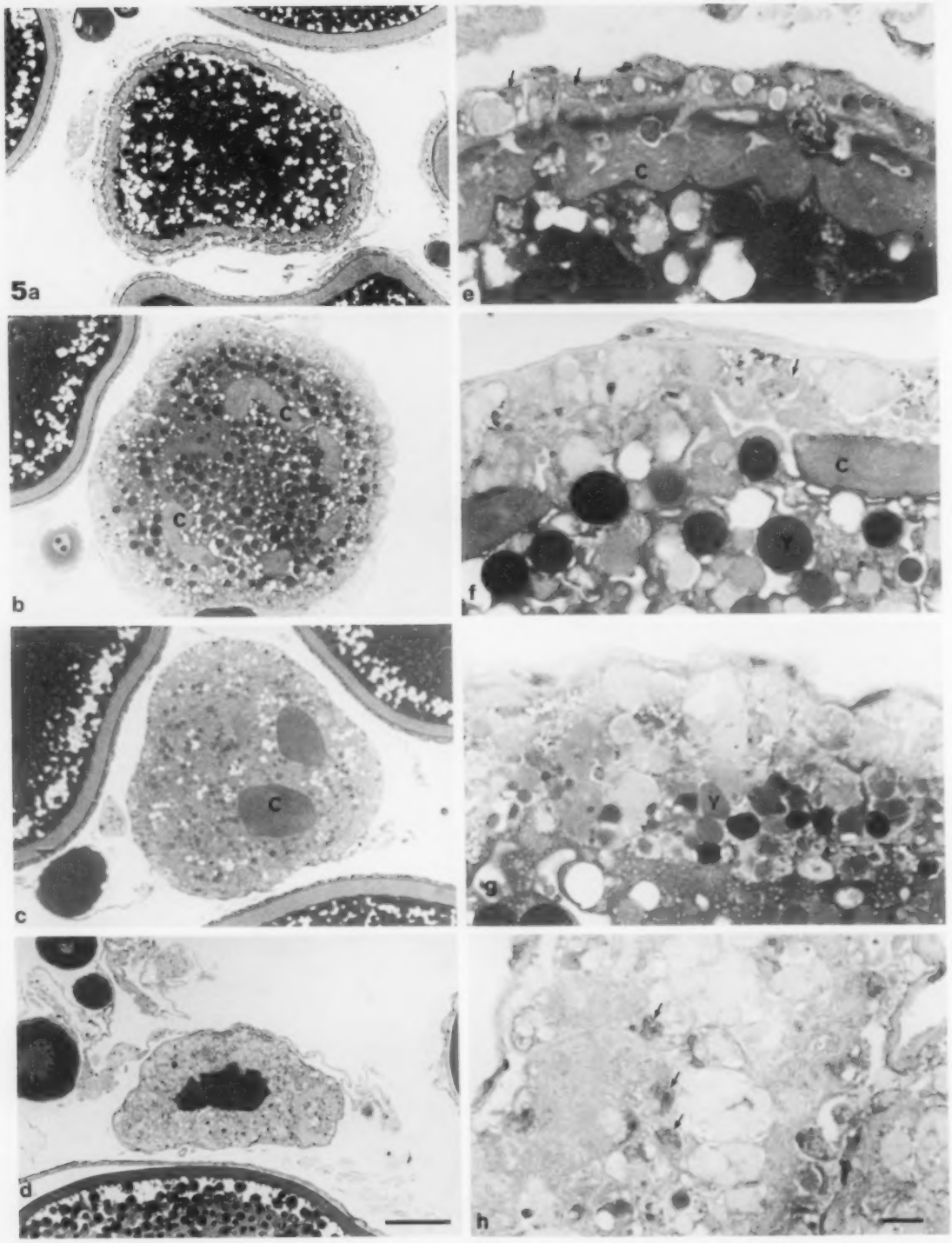

FIG. 5. Light micrographs of different phases of α-atretic vitellogenic oocytes. (a) An early phase, with chorion (C) slightly distorted, but in position. The cytoplasm contains abundant yolk granules. 130×. (b) The chorion has been fragmented and moved into deeper layers. 130×. (c) Chorion (C) remnants are dispersed, and the yolk content is markedly reduced. 130×. (d) A late phase, with very few visible yolk granules. The chorionic material is located in the central part of the oocyte. 130×. Bar = 100 μm (valid for Fig. 5a–5d). (e) An early phase of chorion degradation, with fissures, mainly on the external face. Arrows: follicle cell nuclei. 810×. (f) Later phase, with chorionic fragments and invading follicle cells (arrow). Yolk granules (Y) are still spherical. 810×. (g) Yolk granules degradation, mainly in the cortical zone. 810×. (h) Cytoplasm of a late phase of atresia, with abundant follicle cells (arrows) and no intact yolk granules. 810×. Bar = 10 μm (valid for Fig. 5e–5h).

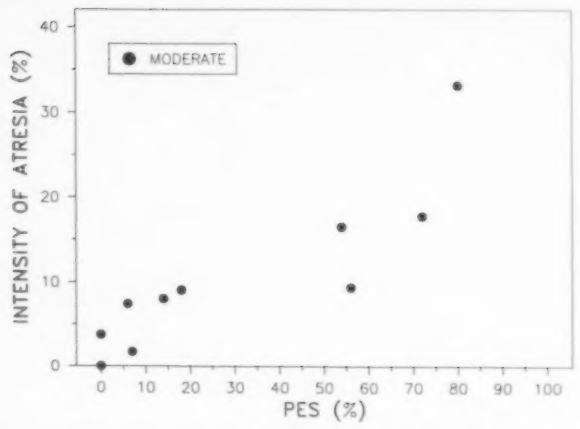

FIG. 6. Relationship between intensity of atresia (α-atretic vitellogenic oocytes) and portion of eggs spawned (PES).

diameter increased. The following regression was established, using prespawning and spawning specimens ($n = 18$) from all four feeding groups, between the fresh diameter (x, 400–800 μm) and the dry weight (y, micrograms) of a vitellogenic oocyte:

$$(4) \quad y = 0.1613 \cdot x - 52.3 \qquad (r^2 = 0.974,\ P < 0.001).$$

Vitellogenic oocyte dry weight was based on ovary dry weight and the number of vitellogenic oocytes present excluding ovaries containing a batch of hyaline oocytes. It was assumed that the estimate of oocyte dry weight was 5% too high due to the weight of stroma (O.S. Kjesbu, unpubl. data). Application of equation (4) shows that Fig. 7d comprises oocyte dry weights of 28 μg (at 500 μm) to 77 μg (at 800 μm). A typical diameter after the beginning of spawning was 750 μm corresponding to 69 μg. Subtraction of this dry weight from the recorded egg dry weight (Fig. 7b) should generally reflect the uptake of material by the developing oocyte during spawning.

Discussion

In recent years, the biomass of many Atlantic cod stocks has declined dramatically and this is particularly true for the Northeast Arctic cod (Sundby and Sunnanå 1990). This decline has focussed attention on recruitment to the parent stock which is highly variable and poorly understood. Successful levels of recruitment are dependent, among other things, on the production of large numbers of good quality eggs. Cod spawning in the northeast Atlantic do not feed to any significant extent (54% of adults at Lofoten and 5–10% of immature cod in the Barents Sea between March and April 1984–90 have empty stomachs (S. Mehl, Institute of Marine Research, Bergen, pers. comm.)). It was noted during the present experiment that appetites for food dropped significantly at the beginning of the spawning period, but Brawn (1962) has shown that captive cod take food later in the spawning period and this may affect egg production (Wootton 1977: *Gasterosteus aculeatus*). In general, however, fish such as the cod with a determinate fecundity are dependent on reserves of protein and fat to promote gonadal maturation, and the present study confirms earlier work (Love 1960; Dambergs 1964; Krivobok and Tokareva 1973) which showed that female cod withdrew protein from the muscle and fat from the liver during the spawning period. In wild plaice (*Pleuronectes platessa*), another determinate spawner, as much as 50% of the total gonadal growth was taken from body reserves (Rijnsdorp 1990). The development of the ovaries of all experimental cod groups depended on the reserves in the white muscle and liver, but in the case of the starved group this dependence started much earlier in the ovary growth cycle. However, the better fed fish produced many more eggs than wild fish and the larger fish are particularly fecund. A 60-cm Northeast Arctic cod has a relative potential fecundity (number of vitellogenic oocytes/somatic weight (somatic weight being defined as whole body weight − ovary weight)) of $325 \cdot g^{-1}$, while one at 120 cm has $600 \cdot g^{-1}$, an increase of 85%. This trend is even more more marked in Norwegian Coastal cod (Kjesbu 1988), and larger Baltic cod (Krivobok and Tokareva 1973) lose relatively more carcass and liver weight than the smaller fish. The conclusion of Eliassen and Vahl (1982) that energy input to the gonad during the spawning period is small when compared with the maintenance requirement (in the present study shown to be about 18 $J \cdot g\ fish^{-1} \cdot d^{-1}$ in 2000-g fish compared with 26 $J \cdot g\ fish^{-1} \cdot d^{-1}$ in 100- to 500-g fish (E. Lied, Institute of Nutrition, Directorate of Fisheries, N-5002 Bergen, unpubl. data)) should be treated with caution, as the fish were small (45 cm), a constant white muscle mass was assumed throughout the year, and data from males and females were combined.

It has been shown that vitellogenesis continues during spawning (the input of fat and protein to the ovary was in the ratio 1:5, showing that it was yolk (Plack et al. 1971)). The mean vitellogenic oocyte diameter is at first small but rises to a maximum size at 10% PES which coincides with the major influx of protein to the ovary. It appears that it is this event and subsequent influxes between batches which continue at a decreasing rate (see also Kjesbu et al. 1990) that determine the final oocyte size. Atretic oocytes have been described in a number of teleost species (Byskov 1978). As evident from the present study, the sequence of events is easily recognised. The theca layers of the follicle, with abundant blood capillaries, are present throughout the process. The follicle cells that invade the oocyte cytoplasm contribute to the process of yolk degradation, and in this manner, material becomes available for other purposes such as final oocyte maturation elsewhere in the ovary. This is supported by the observation that atresia did not appear in the prespawning ovary (except for fish in very poor condition).

Measurements of potential and actual fecundity have not previously been compared in cod. This work shows the actual fecundity to be 20–80% lower than the potential fecundity depending on the nutritional status of the fish. In live fish, however, the crucial point was the estimation of the potential fecundity. Ultrasonic techniques, recently developed at the Austevoll Aquaculture Research Station, give the ovary weight precisely (error ≈5%) (Ø. Karlsen, unpubl. data). This figure, together with the number of vitellogenic oocytes per gram ovary using biopsy techniques, should improve the estimate of the potential fecundity in relation to our method where equation (2) explained 86% of the variation. Also, this technique would be independent of other variables used to calculate the condition factor of the fish. Atresia has been regarded as a mechanism for regulating egg number in fish with an indeterminate fecundity such as the horse mackerel (*Trachurus trachurus*) (Macer 1974). Assessment of the total atresia in the wild population requires knowledge of the duration of atretic oocytes. Hunter and Macewicz (1985) estimated the duration in anchovy

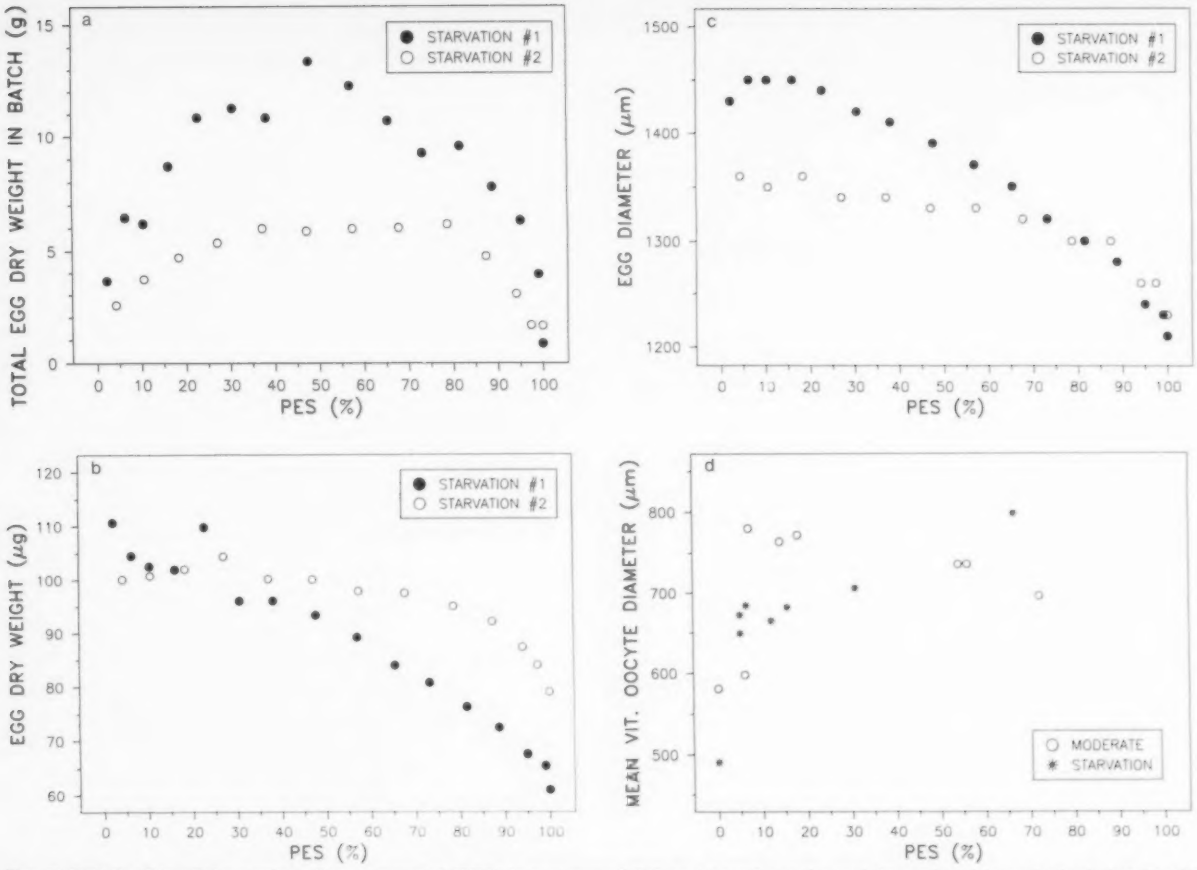

FIG. 7. Relationship of the portion of eggs spawned (PES) in two starved fish to (a) total egg dry weight produced in each single batch), (b) mean individual egg dry weight (n = 50), (c) mean egg diameter (50 fertilized eggs), and (d) PES is related to mean fresh vitellogenic oocyte diameter in starved fish and fish on moderate ration.

(*Engraulis mordax*) to be on average 8 d at 16°C. This compares with 13 d for cod at 8°C, giving an increase in metabolism for each 10°C (Q_{10}) of 1.83 (Q_{10} is typically close to 2 but may vary significantly between species (Brett and Groves 1979)). It is plain that a small standing stock of atretic oocytes because of high turnover rates could significantly reduce the potential fecundity in species with long spawning periods. However, the intensity of atresia in wild cod stocks is as yet unknown.

Results indicate that there are at least two mechanisms in cod regulating the number of vitellogenic oocytes produced prior to spawning. Firstly, the number of previtellogenic oocytes entering the circumnuclear ring phase (Woodhead and Woodhead 1965) formed during the postspawning period (Barr 1963: *Pleuronectes platessa*; Tokarz 1978). This number seems to increase in a linear manner with the weight of the fish (Waiwood 1982), and as their production requires little energy, their number is more a function of ovary size. Secondly, the increased production of previtellogenic oocytes during the autumn, a mechanism described in both the winter flounder (*Pseudopleuronectes platessa*) (Tyler and Dunn 1976) and in the present study to be closely positively correlated with the condition factor of the fish (the quoted total number of previtellogenic oocytes in the ovary should, however, be checked using the more accurate stereological method (Emerson et al. 1990)); there is apparently at that stage of maturity a linkage between development of previtellogenic oocytes and fish nutritional status.

In conclusion the present study shows that the supply of protein from the white muscle and fat from the liver makes further vitellogenesis possible during the spawning period, and this may be augmented by the breakdown products from atretic oocytes such that stored reserves are used to the maximum advantage. Atresia was inversely related to the nutritional status of the fish causing the actual fecundity to be reduced by 20–80% of the potential fecundity. The duration of atretic oocytes, a parameter needed to estimate the total atresia in wild fish, was found to vary from 10 to 13 d at 8°C. The egg size was shown to decrease during the spawning period, and this appears to be related to the declining reserves for vitellogenesis as spawning progresses.

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Hydrocarbon and Metal Contents in a Sediment Core from Halifax Harbour: A Chronology of Contamination[1]

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In a dated core from the Northwest Arm of Halifax Harbour, pollutant hydrocarbon concentrations have increase 100-fold since about 1900 (15–20 cm depth). Aliphatic contaminants characteristic of sewage and urban runoff have had a steady, exponential growth over time, while aromatic hydrocarbon combustion products are currently declining slightly from a subsurface maximum around 1950 (5–10 cm depth). Present levels of these compounds are among the highest reported in the literature. Similarly, contamination of sediments by the metals Cu, Zn, Pb, and Hg has also increased from 1890 to 1970, with maximum levels among the highest reported from other urban and industrialized coastal marine areas in the world. In contrast, the concentrations of natural product hydrocarbons such as squalene and perylene have not changed significantly in this century.

Dans une carotte datée du bras nord-ouest du port d'Halifax, les concentrations d'hydrocarbures polluants ont centuplé depuis 1900 environ (profondeur de 15 à 20 cm). Les contaminants aliphatiques caractéristiques des eaux d'égout et de ruissellement urbaines ont connu une croissance exponentielle régulière dans le temps, tandis que les produits de combustion d'hydrocarbures aromatiques sont en train de chuter légèrement sous un maximum subsurfacique enregistré aux environs de 1950 (profondeur de 5 à 10 cm). Les concentrations actuelles de ces substances sont parmi les plus élevées dont il est question dans la documentation. De même, la contamination des sédiments par des métaux, tels Cu, Zn, Pb et Hg, a aussi augmenté entre 1890 et 1970, des maximums parmi les plus élevés ayant été observés dans d'autres zones littorales marines, urbaines et industrielles, dans le monde. Par ailleurs, les concentrations d'hydrocarbures marchands naturels comme le squalène et le pérylène n'ont pas beaucoup varié au cours du siècle.

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Since its founding in 1749, Halifax Harbour has been developed as a major naval and commercial port with a growing urban population. Chemical contaminants have been deposited in the sediments of Halifax Harbour for at least the past 100 yr as a result of untreated sewage and storm drainage discharge and other waste disposal practices. High concentrations of metals and organic carbon have been found in most of the surface sediments throughout the Harbour, particularly near waste discharge sites (Buckley et al. 1989; Buckley and Hargrave 1989). Sediments deposited near these outfalls or in depositional basins have high rates of oxygen uptake and are chemically reduced immediately below the surface, within the top 2–3 mm (Buckley and Hargrave 1989). Redox potentials (pE) decline with depth, from a maximum of 2.5 at the surface to -2.0 at the bottom of the core. Sulphate reduction is evident by the decrease in dissolved sulphate in pore water from a maximum at the surface of 26 mM to 0 mM at 60 cm depth (LeBlanc et al. 1991). Studies of metal content in sediment cores taken from several areas of the Harbour demonstrated that large reservoirs of contaminant metals (Zn, Cu, Pb, Cd, and Hg) are held in the upper 15–50 cm of sediment (Buckley et al. 1990). In this paper we report the first detailed analyses of hydrocarbon contaminants from a core taken in the Northwest Arm of Halifax Harbour. These data are compared on a geochronological basis with results of analyses for some trace metal contaminants. This allows a history of contamination to be interpreted and assessed relative to urban and industrial growth and the use of fossil fuels and chemical agents.

Sampling and Analytical Methods

Core Sample

A core site was selected in the centre of Northwest Arm (Fig. 1) to sample a sequence of fine-grained chemically reduced mud (99.5% less than 63-μm particle size, pE < 2.5). Analyses of a series of surface grab samples for organic carbon and metals (Buckley et al. 1989; Buckley and Hargrave 1989) indicated that this site would be reasonably representative of contaminated Harbour sediments. In addition, this site was

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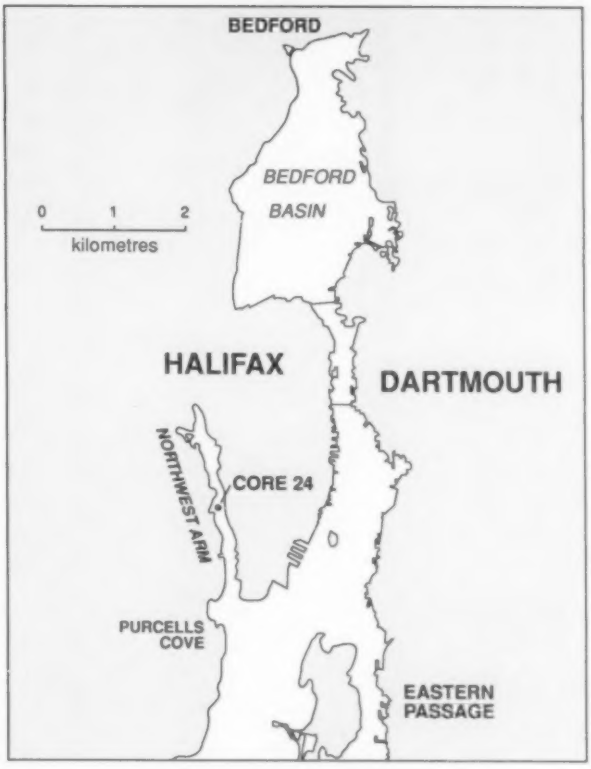

FIG. 1. Halifax Harbour, with location of sediment core 24 in the Northwest Arm.

known to be in an area where little or no disturbance of sediments had occurred as a result of ship traffic and bioturbation (Miller et al. 1989). The core sample No. 24 was obtained in 1989 with a modified Lehigh gravity corer that consisted of a 1.5-m length of PVC pipe (10-cm diameter) with a 75-kg core head weight and a water-tight valve. A stainless steel core catcher was used in the bottom of the core barrel. After the core was retrieved, it was kept in a vertical position, while overlying water was siphoned from the upper part of the core barrel. The core was transported immediately to the laboratory for X-radiography and temporary storage at 4°C. Subsampling was done within 8 h of collection. The core was vertically extruded, with 1-cm-thick samples (approximately 40 cm^3) being taken from the centre of the whole round core every 5 cm for inorganic geochemical analyses. The intervening 4-cm-stick sections were selected for hydrocarbon analyses. Fresh subsamples were immediately taken for water content measurement (from which porosity was determined) and for grain size analysis. Samples for inorganic analyses were freeze-dried. Samples for organic analyses were placed in cleaned glass jars, sealed, and frozen.

^{210}Pb Analyses

One gram of dried sediment was digested in nitric and hydrofluoric acids and then redissolved in 0.5 M hydrochloric acid. This solution together with polonium (^{210}Po and tracer ^{208}Po) was plated by electrochemical deposition onto silver discs (Flynn 1968; Smith and Walton 1980). The discs were analyzed for radioactive Po using surface barrier detectors in an alpha spectrometer. ^{210}Pb activities were determined from these data assuming that negligible postdepositional migration of Po or Pb occurs in the sediments (Crusius and Anderson 1991). In order to determine the ^{226}Ra-supported ^{210}Pb activity, ^{226}Ra measurements were conducted on sediment samples using the radon gas emanation method (Smith and Walton 1980). This method involves the complete acid digestion of a sediment sample and subsequent extraction of ^{222}Rn using a helium carrier gas, followed by the scintillation counting of radon in a photomultiplier-based spectrometer. ^{137}Cs measurements were conducted on 5-g sediment subsamples using nondestructive gamma counting with a hyperpure Ge detector (Smith et al. 1987).

Hydrocarbon Analyses

Just before extraction, samples were thawed, inspected for organisms, and sieved (82-μm mesh). An aliquot was taken for determination of dry weight. Deuterated internal standards were added to wet sediments which were refluxed for 4 h in 1.5 M KOH/CH_3OH. The nonsaponified fraction was extracted with three aliquots of hexane. Following sulphur removal with activated copper, this fraction was separated into f_1 (aliphatic) and f_2 (aromatic) hydrocarbons by column chromatography using 2:1 (w/w) alumina over silica gel (Gearing et al. 1978).

Hydrocarbons were separated, identified, and quantified by high-resolution gas chromatography. A Carlo-Erba HRGC 5160 gas chromatograph was run with helium carrier gas, cool on-column injector, 30 m × 0.32 mm inside diameter fused silica column with bonded methyl silicone (DB5, 0.25-μm film thickness) and flame ionization detector. After a 5-min initial hold at 65°C, the gas chromatograph was temperature programmed at 4°·min^{-1} to 350°C, where it was held for 2 min. The detector temperature was 370°C.

Peaks were quantified by internal standards using a Spectra-Physics 4290 integrator coupled with an Epson Equity I+ computer using the Labnet/Winner chromatographic software. This system allowed detailed examination of baselines and reintegration. Peak areas were generally used for quantification after comparison with peak heights. The unresolved complex mixture in the f_1 fraction was calculated using a solvent baseline and the average of the response factors of the three aliphatic internal standards (n-C_{16}-d_{34}, n-C_{24}-d_{50}, and n-C_{36}-d_{74}). Total aliphatic hydrocarbons were measured chromatographically, being the sum of resolved and unresolved compounds between Kovats indices 1200 and 4000.

Selected samples were further analyzed by GC/MS. The gas chromatograph was a Hewlett-Packard 2890 with an on-column injector and helium carrier gas. A 30 m × 0.32 mm inside diameter fused silica column (DB5) was temperature programmed as follows: (1) initial hold for 3 min at 65°C, (2) 5°·min^{-1} to 100°C, (3) 1°·min^{-1} to 230°C, (4) 3°·min^{-1} to 320°C, (5) final hold for 10 min at 320°C. The GC was interfaced with a TS250 mass spectrometer from Vacuum General (VG) with an EBE configuration run in the electron impact mode (electron energy = 70 eV, filament current = 4000 μA, source temperature = 180°C, resolution = 700, scanning from 50 to 650 daltons at 1 s·$decade^{-1}$). All data were stored and processed using a PDP-11 (Digital Equipment Corp.) and VG software.

Metal and Organic Carbon Analyses

Organic carbon in percent dry weight was determined from washed and dried samples after removal of inorganic carbon by

treatment with 1 M HCl. Percent organic carbon was determined from the weight of the sample before acid treatment with HCl, so that correction for $CaCl_2$ was not required. Instrumental analysis was with a Leco carbon analyzer. Total metal analyses were conducted by atomic absorption spectroscopy after total decomposition, using the modified Buckley and Cranston (1971) method. Accuracy of analytical determinations was verified by analyses of NRC sediment standards BCSS, MESS, and PACS-1 and USGS standard MAG-1. NBS standard 1645 was used for verification of Hg accuracy from analyses by a cold vapour method. Organically bound metal was estimated by leaching the sample with 10% H_2O_2, with neutral adjustment of pH to minimize extraction of sulphides. (LeBlanc et al. 1991). An indication of the efficiency of the oxidizing leach in extracting metal from the organic matter was obtained by statistical evaluation of the relationship between total metal content and organic carbon content. These tests established that the oxidizing leach was specific for organically bound metal (Cu, Zn, and Pb) in about 80% of the samples.

Results and Discussion

^{210}Pb Geochronology

^{210}Pb is produced in the atmosphere by the radioactive decay of radon gas (^{222}Rn) and is transported to surface water by precipitation and dry fallout. Upon entering the water column, it is rapidly scavenged by particles and accumulates as an unsupported and relatively immobile (Crusius and Anderson 1991) excess (above background levels) in the sediments. For the case of a constant sediment accumulation rate, ω (grams per square centimetre per year), and a constant ^{210}Pb flux, F (disintegrations per minute per square centimetre per year), to the sediments (referred to as the CFS model; Smith and Walton 1980), the steady-state distribution of the excess ^{210}Pb activity (disintegrations per minute per gram) is given by

$$(1)\quad A_{Pb-210_{ex}} = \frac{Fe^{-\lambda t}}{\omega}$$

where λ is the radioactive decay constant for ^{210}Pb ($0.031 \cdot yr^{-1}$), and t (years), the time elapsed since sediment deposition, is given by

$$(2)\quad t = \frac{m}{\omega}$$

where m is the mass-depth (grams per square centimetre). The mass-depth scale is determined by integration of the overlying mass of dry sediment at each depth level as determined from the detailed porosity profile for the sediment core. The ^{210}Pb activity decreases exponentially with increasing time and mass-depth according to its half-life of 22.3 yr. The excess ^{210}Pb activity is given by the difference between the total ^{210}Pb activity and the background ^{226}Ra-supported activity. The mean ^{226}Ra activity in the core is 1.00 ± 0.05 dpm·g^{-1}. The excess ^{210}Pb activity is illustrated on a semi-log scale as a function of mass-depth in Fig. 2. From the slope of the linear, least squares fit to these data (weighted by the square of the inverse of the fractional uncertainty of each measurement), a value of 0.063 $g \cdot cm^{-2} \cdot yr^{-1}$ was determined from equations 1 and 2 for the sediment accumulation rate for the core. This corresponds to a sedimentation rate of approximately 0.2–0.3 $cm \cdot yr^{-1}$ at the average sediment densities encountered in the core. These data

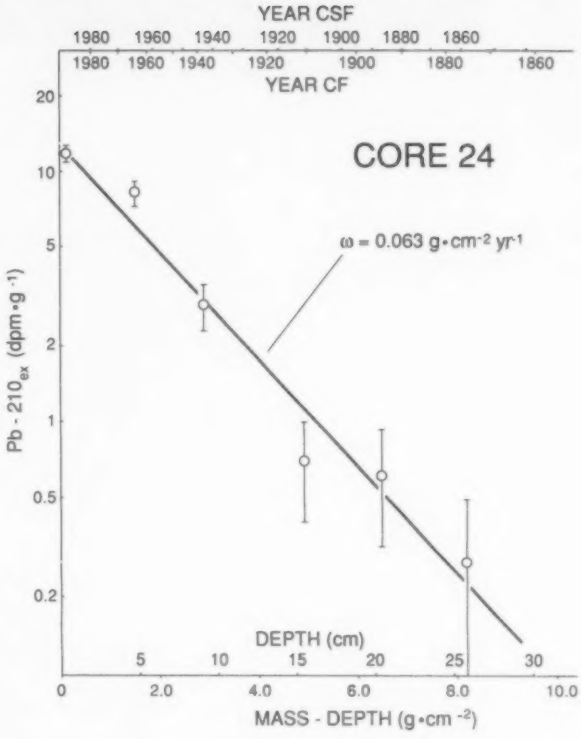

FIG. 2. Plot of excess ^{210}Pb versus depth in the sediment core and mass-depth. Results of two methods of calculating age of sediments are plotted on the upper axis (see text for criteria used to calculate age).

permit the determination of a geochronology for the core using equation 2, which is scaled at the top of Fig. 2. An alternative model for determining sediment geochronologies is the constant flux (CF) model in which the ^{210}Pb flux (F in equation 1) is assumed to be constant (Robbins 1978; Smith and Schafer 1987). Because certain dynamic sediment regimes are subject to disturbances and slumps that can produce anomalies in sedimentary chemical profiles, the CF model is particularly useful in the interpretation of chemical signals in such systems. This approach has been used extensively, for example, in the interpretation of metal profiles in Halifax Harbour sediments (Buckley et al. 1990). However, in the present case, the CFS model provides a geochronology in reasonable agreement with the CF model (Fig. 2), and the former simpler model is used in this paper.

Although X-radiographs of the sediment core did not indicate the presence of worm tubes or other evidence of either physical mixing or bioturbation in these anoxic sediments, postdepositional mixing of ^{210}Pb must be considered when this isotope is used as a geochronological tracer. ^{137}Cs is a fission product first introduced into the environment as a consequence of atmospheric nuclear weapons test conducted in the early 1950s. In well-preserved, unmixed marine sediments the initial appearance of elevated levels of ^{137}Cs will occur at the 1952–54 age horizons as determined by ^{210}Pb dating, while in bioturbated sediments, ^{137}Cs will generally have undergone downward transport below the 1950 (^{210}Pb) horizon. Under this

latter circumstance, the ^{210}Pb aging model must be modified to include a mixing component (Robbins 1978). ^{137}Cs measurements conducted on sediment samples from core 24 indicated activities of 1 dpm·g^{-1} or greater above the 6-cm level (1965 ± 3 yr), decreasing to values less than the detection limit (<0.08 dpm·g^{-1}) below the 10-cm level (1939 ± 5 yr). The limited resolution of the ^{137}Cs and ^{210}Pb data does not completely preclude mixing in the upper 5 cm of core 24. However, more tracer studies on other Halifax Harbour cores tend to confirm the absence of significant postdepositional mixing in the sediment regimes from the Northwest Arm, thereby permitting the use of a relatively simple, CFS, ^{210}Pb dating model.

Extrapolation of the least squares fit (Fig. 2) to the ordinate permits the determination of the *y*-intercept ($= F/\omega$, equation 1) and the ^{210}Pb flux, F, across the sediment–water interface. The experimentally determined flux of 0.9 dpm·cm^{-2}·yr^{-1} falls within the range of approximately 0.90–1.00 dpm·cm^{-2}·yr^{-1} estimated for the atmospheric ^{210}Pb flux at the latitude of New York City (Turekian et al. 1977). The ratio of the experimentally determined to the measured atmospheric flux represents the "focusing factor" which is a measure of the accumulation of particle-reactive substances (such as ^{210}Pb and many contaminants) in a specific sediment regime, relative to their input flux. ^{210}Pb inputs to the Northwest Arm of Halifax Harbour would be mainly from direct atmospheric deposition with additional, probably smaller, advective inputs from coastal waters and freshwater runoff. If atmospheric deposition represents the principal source of ^{210}Pb in the sediments, then the good agreement between the measured and the atmospheric ^{210}Pb fluxes implies that the sediment regime, characterized by core 24, indeed provides an accurate record of the accumulation and retention of particle-reactive substances deposited from the overlying water column.

Aliphatic Hydrocarbons

Aliphatic hydrocarbons include a complex assemblage of compounds whose relative distributions can be used to identify the sources of the organic matter present (Ehrhardt and Blumer 1972). The hydrocarbon patterns of terrestrial plants, marine plankton, and petroleum are distinct. Relatively low concentrations of certain individual hydrocarbons such as n-C_{15}, n-C_{17}, pristane, n-C_{29}, and n-C_{31} are produced biologically. The presence of fossil fuels such as coal and petroleum and their byproducts can be recognized by higher levels of a very much more complex group of compounds. Aliphatics have been used to distinguish terrestrial from marine organic matter and to quantify pollution from oil spills and from chronic pollution via sewage, seeps, and storm runoff (Clark and Blumer 1967; Gearing et al. 1976; Farrington and Tripp 1977; Barrick et al. 1980; Gearing et al. 1980; Hoffman and Quinn 1983; Readman et al. 1986).

The concentrations of total aliphatic hydrocarbons found in this core (see Table 1 and Fig. 3A) decline smoothly with increasing depth. The levels near the surface (maximum 1770 μg·g dry weight^{-1}) are quite high. The elevated concentrations may partially reflect the anoxic conditions and high organic carbon content, which tend to preserve and concentrate lipophilic compounds such as hydrocarbons. However, the change over time in hydrocarbon concentrations (by a factor of 100) is much greater on a relative scale than the 20% change in organic carbon and occurs over a different time scale. This suggests that changes in input rather than changes in preservation determine the pattern noted. Similarly high values have been reported for other polluted areas: up to 1800 μg·g^{-1} in the New York Bight (Farrington and Tripp 1977), around 1600 μg·g^{-1} in Lake Washington (Wakeham and Carpenter 1976), and 730–2300 μg·g^{-1} in the Southern California Bight (Venkatesan et al. 1980). Concentrations of greater than ~500 μg·g^{-1} are thought to cause ecological damage (Olsen et al. 1982). Levels in the six samples from 20 to 50 cm depth (deposited before about 1900) average 18 μg·g^{-1}, within the range found for relatively clean areas in the Gulf of Mexico (Gearing et al. 1976; Kennicutt et al. 1987) but slightly higher than the values of 1–5 μg·g^{-1} measured on the Scotian Shelf and other oceanic environments (Farrington and Tripp 1977; Keizer et al. 1978). Boehm (1984) reported that sediments in the Georges Bank region contained 4–5% organic carbon and averaged 3 μg hydrocarbons·g^{-1}.

This pattern of very high values in the top three samples (post-1910), intermediate levels at 15–20 cm 1880–1910), and relatively unchanging, low levels below 20 cm (pre-1880) can be seen (with some minor variations) in all of the pollution-related individual hydrocarbons examined. Another, much smaller relative maximum in some anthropogenic hydrocarbons was noted at 35–40 cm (about 1800).

The most abundant pollution-related hydrocarbons in this core make up the so called unresolved complex mixture (UCM). This group of compounds is thought to consist of branched and cyclic hydrocarbons which are relatively resistant to biodegradation (Blumer et al. 1970; Gough and Rowland 1990). Its occurrence suggests the presence of degraded fossil fuels, although some biological sources have also been hypothesized (Venkatesan and Kaplan 1982). The concentration of the UCM has increased exponentially by 100-fold over time in this core, constituting the majority of the increase in total aliphatics (Table 1; Fig. 3A). Surface values are quite high (1570 μg·g^{-1} after 1960), similar to values from other enclosed areas near population centres. The exponential increase with time since the turn of the century is a typical pattern reflecting increasing human usage of fossil fuels. A similar curve was reported for a core from the southern California shelf, collected near petroleum production and refining facilities (Venkatesan et al. 1980).

There is a lesser (10-fold) increase in the resolved aliphatic hydrocarbons with time since around 1940, particularly evident in the top two samples (Table 1). This increase reflects the presence of degradation products such as pentacyclic triterpanes which are found in fossil fuels but not in uncontaminated recent sediments (Broman et al. 1987). The ratio of chromatographically resolved to unresolved hydrocarbons changes dramatically from values less than 0.2 in the top four samples (post-1900) to values greater than 1 lower down in the core. Ratios around 0.2 are typical of contaminated areas, for example on the Scotian Shelf just off Halifax (Keizer et al. 1978) and in the Gulf of Mexico (Gearing et al. 1976).

The straight-chain (normal) alkanes are highest at the surface (21 μg·g^{-1}, 0–5 cm, post-1960) and decline with depth (~4 μg·g^{-1}), 15–35 cm, 1920–1820; Table 1). A small secondary maximum (7.5 μg·g^{-1}) occurs below 35 cm (pre-1820). These concentrations are greater than the 2.1 μg·g^{-1} reported for the Atlantic continental shelf off New England (Venkatesan et al. 1987) where there is only 1.6% organic carbon.

TABLE 1. Concentrations of some representative hydrocarbons in a Northwest Arm sediment core (Halifax Harbour).

Estimated age:	1977	1958	1933	1905	1876	1850	1820			
Average depth (cm):	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	43.5	47.5
% organic carbon:	6.1	5.5	4.4	4.0	4.0	4.1	4.6	4.6	4.7	5.0
Aliphatic hydrocarbons										
Total[a]	1770	940	440	93	13	17	11	34	17	18
UCM[a]	1570	780	420	80	3.2	1.8	0.9	14	1.1	0
Resolved[a]	200	160	24	13	9.4	14.7	9.9	20	16	18
Total *n*-Alkanes[a]	21	8.4	6.6	3.5	3.0	4.4	3.5	7.5	6.2	6.2
n-Alkanes (C_{16}–C_{20})[a]	1.0	0.6	0.9	0.5	0.3	0.6	0.4	0.7	0.5	0.6
n-Alkanes (C_{21}–C_{30})[a]	8.8	3.5	3.3	2.3	2.3	3.2	2.6	5.4	4.5	4.5
n-Alkanes (C_{31}–C_{40})[a]	11	4.3	2.4	0.7	0.4	0.6	0.5	1.4	1.2	1.1
n-C_{18}[b]	300	220	220	86	32	46	30	90	40	40
n-C_{19}[b]	300	130	240	260	210	410	300	430	320	420
n-C_{27}[b]	1060	520	430	340	390	470	430	1050	900	800
n-C_{28}[b]	770	220	190	72	54	66	50	280	140	100
n-C_{36}[b]	650	290	170	14	nd	nd	2	7	5	nd
Pristane[b]	1480	590	550	170	37	46	30	70	30	20
Phytane[b]	1060	400	290	72	16	26	15	40	20	20
Ratios										
Pristane/phytane	1.4	1.5	1.9	2.4	2.3	1.8	2.0	1.8	1.5	1.0
Resolved/UCM	0.13	0.21	0.06	0.16	2.9	8.2	11.0	1.4	14.5	∞
Aromatic hydrocarbons										
Combustion products[a]	20.4	26.7	18.4	6.9	0.7	0.2	0.5	0.4	0.4	0.3
Phenanthrene[b]	3400	3800	2800	800	42	13	34	60	30	15
Anthracene[b]	830	870	700	210	13	6	14	30	17	9
Fluoranthene[b]	4700	5500	3300	1300	100	13	17	30	17	nd
Pyrene[b]	4000	5500	3600	1400	84	13	17	30	25	nd
Benzo[*a*]anthracene[b]	1600	1500	1500	660	50	nd	190	nd	nd	nd
Chrysene[b]	1800	1900	1700	600	250	70	80	300	194	170
Benzofluoranthenes[b]	3500	6000	3100	1000	80	20	85	nd	nd	nd
Squalene[b]	400	370	300	320	310	250	480	860	680	470
Benzo[*e*]pyrene[b]	1100	1200	1200	420	25	6	10	nd	20	23
Benzo[*a*]pyrene[b]	1800	2600	1900	660	33	6	10	nd	20	15
Perylene[b]	530	500	500	370	170	210	560	751	510	430
Indenopyrene[b]	1000	1300	1100	370	25	20	20	20	65	70

[a]$\mu g \cdot g$ dry weight^{-1}, ppm.
[b]$ng \cdot g$ dry weight^{-1}, ppb.

The three molecular-weight ranges of *n*-alkanes have different possible origins. Compounds with 16–20 carbon atoms can arise from algae or from petroleum. Their concentrations do not change greatly with depth in this core (Fig. 3B). The majority of the *n*-alkanes fall in the range C_{21}–C_{30}, which can originate from the cuticular waxes of terrestrial plants or from petroleum. This group shows the same distribution with depth (Fig. 3B) described for total *n*-alkanes. Recent biological products are usually distinguished from fossil fuel *n*-alkanes by their pattern, particularly the ratio of hydrocarbons with an odd number of carbons (predominant in biological samples) to those with an even number of carbon atoms. These carbons preference indices or CPI values decline from biological ratios of 7–10 in the lower, older samples to values typical of oil (around 1) in the top 15 cm (post-1920). This can be clearly seen in the depth profiles of *n*-C_{18} and *n*-C_{19} (Fig. 4A). The odd-carbon alkane declines slightly in concentration as the sediments become younger, possibly reflecting a decline in algal production. The even-carbon alkane, on the other hand, increase 5- to 10-fold since 1920. This change in relative concentrations of two hydrocarbons with similar physical and chemical properties strongly suggests recent increased inputs of fossil fuel hydrocarbons, either directly via spills or indirectly via runoff and sewage effluents.

The ratio of these two *n*-alkane groups has been used to indicate the ratio of natural inputs from terrestrial (C_{21}–C_{30}) sources to those from marine (C_{16}–C_{20}) sources (Gearing et al. 1976); ratios of 4:1 in Halifax Harbour are significantly higher than the ratios of 2:1 off the Mississippi River and 1:1 off Florida. Thus, the Halifax Harbour ratios show a predominance of terrestrial material.

The third group of *n*-alkanes (C_{31}–C_{40}), unlike the lower molecular weight *n*-alkanes, increases significantly toward the surface (Fig. 3B). These compounds are virtually absent in the oldest samples, but increase sharply after 1920. No clear consensus has been reached in the literature on the origin of these compounds. In this core, their distribution correlates with that of pollution hydrocrabons. They may also be produced by bacteria.

The isoprenoids phytane (Fig. 4A) and pristane also reflect the level of pollution, increasing up to 50-fold in the top four samples. The ratio of pristane to phytane changes little throughout the core (Table 1), indicating relatively little contribution of biogenic pristane to these sediments.

In summary, the aliphatic hydrocarbons in the upper four samples (post-1920) are dominated by degraded fossil fuel compounds (UCM, pentacyclic triterpanes, *n*-alkanes with CPI around 1, and a suite of isoprenoids), which are most probably

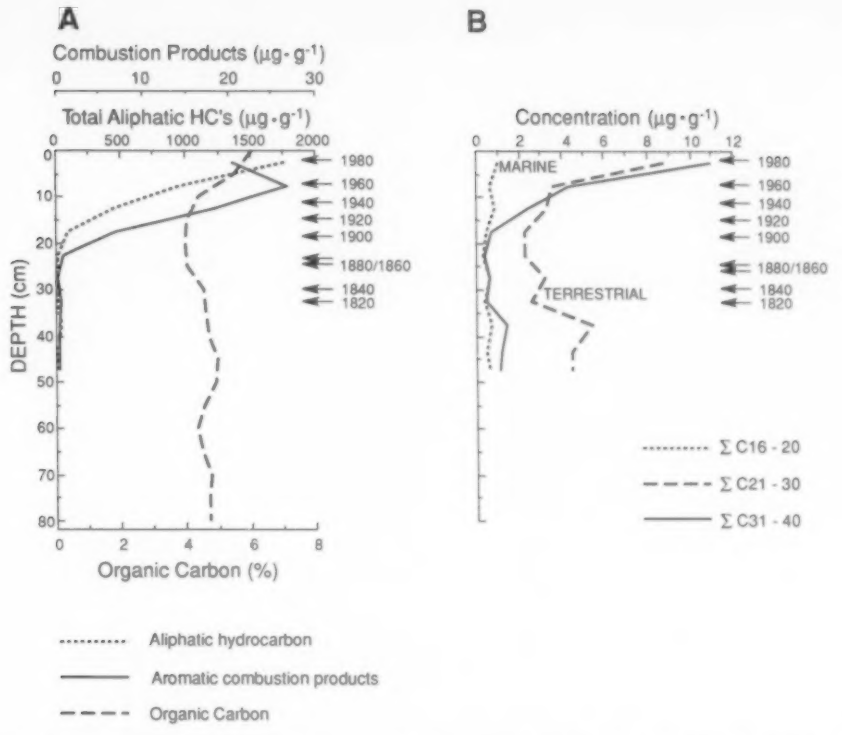

FIG. 3. Profiles of (A) total aliphatic hydrocarbons, combustion products, and total organic carbon and (B) *n*-alkanes in sediment core 24. Age of sediments from excess ^{210}Pb and CFS model is shown to the right.

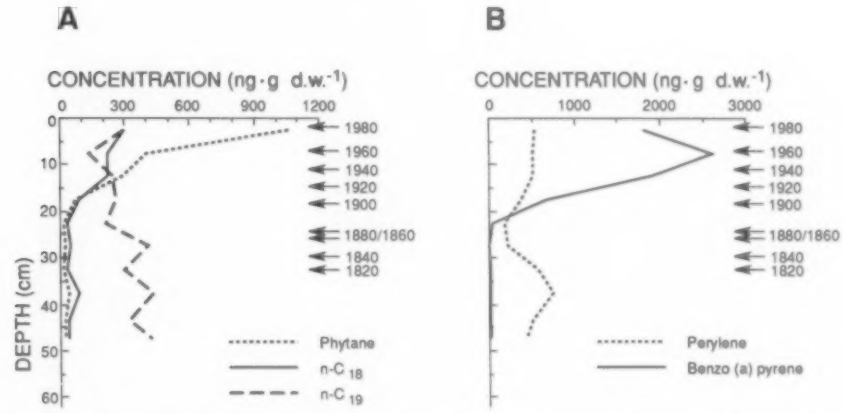

FIG. 4. Profiles of (A) aliphatic hydrocarbons *n*-C_{18}, *n*-C_{19}, and phytane and (B) aromatic hydrocarbons perylene and benzo[*a*]pyrene in sediment core 24.

derived from sewage and urban surface runoff. Their concentrations have increased exponentially with time. Sediments deposited before 1900 (from 25 to 50 cm depth) have relatively low levels of aliphatic hydrocarbons, with high ratios of resolved to unresolved compounds and high CPI values, indicating terrestrial plants as the principal source. A small secondary maximum is found at 35–40 cm (pre-1820), consisting of terrestrial and pollution hydrocarbons. It is probably the result of high storm runoff or a similar episodic event.

Aromatic Hydrocarbons

Complex assemblages of polycyclic aromatic hydrocarbons (PAHs) are found in many recent marine sediments (Youngblood and Blumer 1975; Laflamme and Hites 1978; Lake et al. 1979; Prahl and Carpenter 1983; Barrick and Prahl 1987). They are of environmental concern because many of their component compounds, such as benzo[*a*]pyrene, are carcinogenic.

The principal source of PAHs is the incomplete combustion of organic material, with the composition of the PAH assem-

TABLE 2. Comparison of PAH concentrations ($ng \cdot g^{-1}$).

Location	Reference[a]	Combustion products[b]	Pyrene	Benzo[*a*]pyrene
Sydney Harbour	12	280 000	33 000	28 000
Baltimore Harbour	1	169 000	57 600	1 050
Charles River, MA	2	87 000	13 000	
Halifax Harbour, 5–10 cm	**This study**	**26 700**	**5 500**	**2 600**
San Francisco Bay	3	12 000		
Severn Estuary, UK	4	8 000	1 400	470
LaPlate Harbour, Argentina	5	6 000	1 400	200
New York Bight	2	5 800	1 300	
Upper Penobscot Bay	6	6 000	450	490
Tokyo Bay	7		600	500
Lake Michigan	8	5 000	600	300
Gdansk Harbour, Poland	9	3 000	46	
Puget Sound, Seattle	10	1 300	88	
Gulf of Maine	2	540	100	
Halifax Harbour, 45–50 cm	**This study**	**300**	**nd**	**15**
Pacific Shelf	11	290	53	25
Atlantic Abyssal Plain	2	55	4	nd

[a]References: 1, Fostor and Wright (1988); 2, Laflamme and Hites (1978); 3, Chapman et al. (1987b); 4, Thompson and Eglinton (1978); 5, Colombo et al. (1989); 6, Johnson et al. (1985); 7, Ohta et al. (1983); 8, Helfrich and Armstrong (1986); 9, Lamparczyk et al. (1988); 10, Barrick and Prahl (1987); 11, Prahl and Carpenter (1983); 12, Kieley et al. (1988).
[b]Sum of nine products used in this study.

blage being determined partly by its temperature of formation. Higher temperatures and more complete combustion produce higher proportions of parent aromatics with fewer substituted carbon side chains. PAHs from oils and coals (produced from organic matter over millions of years at relatively low temperature) are highly substituted whereas those from fires have fewer carbon side chains and those from high-temperature industrial processes are almost entirely parent compounds.

The majority of PAHs in the Halifax Harbour core are unsubstituted; some compounds with one or two carbon side chains are present. The overall pattern reflects an accumulation of combustion products transported via the atmosphere and sewage (Bjorseth et al. 1979; Wild et al. 1990). A convenient way of comparing concentrations of such PAHs is by using the sum of several parent compound "combustion products." The exact compounds used for this calculation vary slightly from study to study, but generally include 9–12 unsubstituted hydrocarbons. Here we have summed phenanthrene, fluoranthene, pyrene, benzo[*a*]anthracene, chrysene, benzo[*b*]fluoranthene, benzo[*k*]fluoranthene, benzo[*e*]pyrene, benzo[*a*]pyrene, and indenopyrene.

The sum of combustion products changes nearly 100-fold in the core (Table 1; Fig. 3A). As with the pollutant hydrocarbons, it is high in the top four samples (post-1900) and low in the bottom six samples. However, instead of declining steadily with depth like the UCM, the aromatic combustion products have a subsurface maximum at 5–10 cm (1940–60). Subsurface maxima have often been noted (Ohta et al. 1983); the recent decrease is thought to arise from a shift away from wood and coal burning in the last 40 yr.

The levels of combustion products at the top of this core are extremely high (20–27 $\mu g \cdot g^{-1}$ in the top 15 cm). This is considerably higher than the 5.37 $\mu g \cdot g^{-1}$ found near the mouth of the Northwest Arm (S. MacKnight, Land and Sea Environmental Consultants, Ltd., Dartmouth, N.S., pers. comm.) but approximates the range for other surface samples from other parts of Halifax Harbour that ranged from less than 1.0 to 36.3 $\mu g \cdot g^{-1}$ (Tay et al. 1991; S. MacKnight, pers. comm.). Extreme concentrations of 1890 $\mu g \cdot g^{-1}$ (S. McKnight, pers. comm.) have been found near specific sources, such as an ash pit at a thermal electric plant. Chapman et al. (1987a) have estimated that sedimentary concentrations of 4–10 μg PAHs$\cdot g^{-1}$ can cause measurable biological changes. The present-day concentrations of PAHs in Halifax Harbour are considerably higher than those reported for many other highly polluted areas such as San Francisco Bay, the New York Bight dump site, Tokyo Bay, and Puget Sound near Seattle (Table 2) but are well below the concentrations of 150–280 $\mu g \cdot g^{-1}$ measured in the South Arm of Sydney Harbour, Nova Scotia (Kieley et al. 1988), or the 200 $\mu g \cdot g^{-1}$ measured in subsurface sediments from the Saguenay Fjord in Quebec (Smith and Levy 1990). In contrast, the levels found in the bottom 30 cm of the Halifax core (average 0.4 $\mu g \cdot g^{-1}$) are similar to values reported from clean, offshore areas (see Table 2).

The same trends noted for total combustion products can also be seen in individual aromatic hydrocarbons such as pyrene (Table 1) and benzo[*a*]pyrene (Table 1; Fig. 4B). The maximum concentrations of these compounds in this sediment core (5500 and 2600 $ng \cdot g^{-1}$) are similar to average values reported for London sewage sludge (7200 and 2800 $ng \cdot g^{-1}$; Wild et al. 1990) and higher than those for most surface sediments from other parts of Halifax Harbour (pyrene concentrations up to 2530 $ng \cdot g^{-1}$ and benzo[*a*]pyrene up to 1320 $ng \cdot g^{-1}$; S. McKnight, pers. comm.).

Two natural product hydrocarbons in the f_2 fraction are squalene (Venkatesan and Kaplan 1982) and perylene (Aizenshtat 1973; Venkatesan 1988). Neither of these compounds changes in concentration with time in the same way as the anthropogenic compounds, indicating that the basic physical environment has not changed, but the anthropogenic compounds have simply been added to the natural contribution of hydrocarbons. The concentration of perylene is similar to that in the anoxic sediments of Lake Washington, which are about 5% organic carbon (Barrick and Prahl 1987).

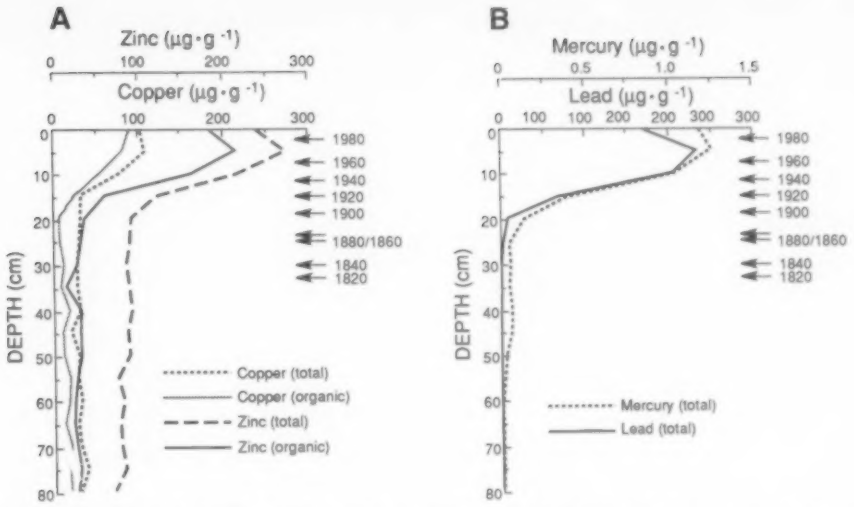

FIG. 5. Profiles of (A) total Cu and Zn, and organically bound (defined by H_2O_2 extraction) Cu and Zn and (B) total Pb and Hg in sediment core 24.

Metal Profiles

The concentrations of the metals Cu, Zn, Pb, and Hg in the core exhibit some characteristics which are similar to those of the hydrocarbons. All of these metals (except organically bound Cu) appear to reach a maximum concentration at about 5 cm depth in the core (Fig. 5). Concentrations then decline rapidly to 20 cm depth, before appearing to reach background levels. These variations occur in spite of the fact that the sediment texture throughout the core is very consistent, the mud content (silt plus clay) being $99.5 \pm 0.2\%$. The mean grain size for all samples in the core was 7.1 ± 1.7 μm, with no significant difference between the upper and lower sections of the core.

The maximum concentration of total Zn in the core is about 1.2 times the mean concentration found in surface sediments from other parts of Halifax Harbour (Buckley and Hargrave 1989). Similarly, the maximum concentration of total Cu and Hg is about 1.3 times, and the maximum total Pb is about 1.5 times, the mean for all surface sediments in the Harbour. All of these contaminants are at concentrations well above the mean levels (by factors of 1.4–6.1) found in other coastal and estuarine areas in eastern Canada (Buckley and Hargrave 1989).

Of the metals measured in this study, the maximum total concentration found in the Northwest Arm core is about the same, or significantly higher (with a few exceptions), than the maximum concentration found in sediment cores from other contaminated coastal and estuarine environments (Table 3). The highest Cu concentration found in cores from Narragansett Bay is about twice the maximum found in the Northwest Arm core, but Zn and Pb contents are higher in the Northwest Arm core. Zn in cores from Chesapeake Bay is slightly higher than in the Northwest Arm core, but Cu and Pb are much lower in Chesapeake Bay cores. All three metals, Cu, Zn, and Pb, are much higher in the Northwest Arm core as compared with cores taken from the sedimentary basins off the southern California coast near Los Angeles (Bruland et al. 1974).

The concentration profiles of the operationally defined organically bound metals Cu and Zn generally follow the characteristics of total metal concentrations in the Northwest Arm core (Fig. 5A). In the upper part of the core (upper 15 cm) the organically bound Cu concentration is $76 \pm 6\%$ of the total metal concentration, but below 15 cm depth, the organically bound metal content is only $46 \pm 15\%$ of the total Cu. Similarly, the organically bound Zn is $71 \pm 12\%$ of the total Zn in the upper 15 cm, but falls to $34 \pm 5\%$ of the total in the lower part of the core. These data suggest that the major increase in the Cu and Zn concentration in the upper part of the core is due to the addition of organically bound metal, probably originating from the addition of untreated sewage to the Harbour.

History of Contamination

The data in Fig. 3–5 clearly illustrate trends in contamination over time. The ^{210}Pb-derived chronology shows that twentieth century deposition is confined to the upper 18 cm of the core. Only slight indications exist for any detectable contamination in nineteenth century sediments below 20 cm depth in the core. Aromatic combustion products began to accumulate in the Harbour sediments around the end of the nineteenth century. This may be the first indication that coal and wood combustion products were entering the Northwest Arm as a result of expanding urbanization in the city of Halifax. There is a rapid increase in combustion product residues such as pyrene up to the late 1950s and then a decline in the more recent sediments at the top of the core. This peak concentration and decline may reflect the shift away from use of coal and wood fuels in the 1950s.

Aliphatic anthropogenic compounds increased exponentially beginning about 1910 with no decline near the surface, reflecting constantly increasing input of sewage during a period of increasing population growth around the Northwest Arm.

Metal profiles (Fig. 5) provide a similar history to that of the hydrocarbon residues. All metals begin to show an increase in concentration at the end of the nineteenth century, and all metals except organically bound Cu reach a peak at about 1970. This characteristic of increasing metal content between about 1890 and 1970 is very similar to that found in a core from Narragansett Bay (Goldberg et al. 1977), lake sediments (Robbins et al. 1990), and coral records (Shen and Boyle 1987).

TABLE 3. Comparison of metal concentrations in coastal estuarine systems.

Location	Reference[a]	Cu ($\mu g \cdot g^{-1}$)		Zn ($\mu g \cdot g^{-1}$)		Pb ($\mu g \cdot g^{-1}$)		Hg ($\mu g \cdot g^{-1}$)	
		Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.
Derwent Estuary, Australia	1	130	9980	600	9900	40	1700		
UK estuaries	2	185	2400	400	3300	220	2000		
San Francisco Bay	3	90	400	450	1800	280	2950		
Halifax Harbour surface sediments	4	91	1910	230	726	161	1440	1.0	10.6
Mersey, England	5	94	144	422	627	138	205	3.01	6.2
Long Island Sound/ Raritan Bay	6	60	1000	40	800	65	1000		
Southern California coastal, surface sediments	7	80	800	210	2500	60	500		
Canso Strait, N.S.	8	24	53	90	310	63	120	1.64	4.10
Halifax Harbour core	**This study**		**109**		**274**		**231**		**1.25**
Narragansett Bay core	9		220		260		140		
Septiba Bay, Brazil	10	20	180			23	80		
Chesapeake Bay core sediments	11	47	52	274	305	65	71		
Miramichi, N.B.	12		21	44	198	326		0.13	0.40
Southern California coastal, core sediments	13	39	44	99	130	16	28		
Scotian Shelf	14	20	50	69	103				

[a]References: 1, de Forest et al. (1978), 2, Bryan et al. (1980); 3, Luoma and Phillips (1988); 4, Buckley and Hargrave (1989); 5, Langston (1986); 6, Greig et al. (1977) and Greig and McGrath (1977); 7, Katz and Kaplan (1981); 8, Cranston et al. (1974); 9, Goldberg et al. (1977); 10, De Lacerda et al. (1987); 11, Goldberg et al. (1978); 12, Wiley and Fitzgerald (1980); 13, Bruland et al. (1974); 14, Buckley and Cranston (1991).

The Northwest Arm metal profile during the twentieth century is similar to that of combustion products such as pyrene. This might suggest that some of the metals are derived from combustion products. The ^{210}Pb geochronology reflects the atmospheric Pb source function associated with the combustion of leaded gasoline, which peaked in approximately 1970 and has declined rapidly to the present day (Edgington and Robbins 1976; Eisenreich et al. 1986). However, Pb was extensively used in marine paints as a spreading and sealing agent up until about 1970 (James F. Lahey Ltd, Queen St. Dartmouth, N.S., pers. comm.). Anomalous concentrations of Pb have been found in marine sediments adjacent to shipyards and solid waste sites at several locations in Halifax Harbour (Buckley and Hargrave 1989). Two large yatch clubs are located in the Northwest Arm near the site where this core was taken. Although anthropogenic Pb in sediments near urbanized environments is often ascribed to gasoline and fuel combustion sources, marine paint sources probably made significant, if unresolved, contributions to Halifax Harbour sediments.

Hg was also commonly used in water-based paints as a fungicide prior to the 1970s (D'Itri and D'Itri 1977), and this metal has been found in high concentrations (up to 10.5 $\mu g \cdot g^{-1}$) in sediments adjacent to major untreated sewer outfalls at several locations in Halifax Harbour (Buckley and Hargrave 1989). The source of this contamination may be both domestic and institutional use of bleaches and disinfectants, as well as some losses from research and medical institutions such as hospitals and dental clinics (D'Itri and D'Itri 1977). Both Cu and Zn are still used in common marine paints and preservatives, but their proportional use may have declined in the past few years, as they are being replaced by other chemical agents. These changes in common use of the metals appear to be reflected in the decline in concentration of these metals in the sediments deposited over the last two decades.

In conclusion, analyses of hydrocarbon residues and metals in a dated core from an undisturbed sedimentary basin in Halifax Harbour clearly demonstrate that the sediments have been accumulating fuel residues and industrial wastes for the past 100 yr. The level of contamination in these sediments is amongst the highest recorded for coastal marine areas in the world. Although the input of some specific contaminants such as aromatic combustion products and some metals (Zn, Pb, and Hg) has declined over the last two decades, the rate of aliphatic hydrocarbon and organically bound Cu accumulation appears to be increasing, probably as a result of increasing sewage discharge.

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Effects of Prolonged Flooding on Nektonic Invertebrates in Small Diked Marshes[1]

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This study examined the response by nektonic invertebrates to prolonged flooding of a series of experimental marshes in the Delta Marsh in south-central Manitoba. Prior to flooding, nektonic invertebrate densities, biomass, and numbers of taxa were at their highest levels during midsummer in open-water sites with dense submersed vegetation; during the same period, nekton levels within the experimental marshes were minimum in stands of emergent vegetation. These differences appear to be related to available habitat structure and dissolved oxygen concentrations. Flooding to 1 m above normal eliminated the submersed vegetation and existing emergent vegetation. This resulted in a single large input of litter at the time of flooding with little or no subsequent input during flooding. The herbivore–detritivore functional group reached high levels early in the first year of flooding and remained high until late in the second year of flooding. The predator–parasite group did not exhibit a similar increase following flooding. Changes in the amount of plant litter available as both food and habitat affected these changes in the nekton following flooding. Wind-induced water currents also probably had an effect on nekton distributions during the flooding period.

La présente étude porte sur la réaction d'invertébrés nectoniques à l'inondation prolongée d'un groupe de marais expérimentaux du Delta Marsh situé dans le centre-sud du Manitoba. Avant l'inondation, les densités, biomasses et nombres de taxons d'invertébrés nectoniques ont atteint leur valeur maximale à la mi-été en eaux libres densément peuplées de plantes submergées alors que; durant la même période, ces valeurs ont été minimales dans les marais expérimentaux peuplés de plantes émergées. Ces écarts semblent attribuables à la structure de l'habitat et à la concentration d'oxygène dissous qui existent dans les deux milieux. Une inondation portant le niveau de l'eau à 1 m de plus que la normale a entraîné l'élimination de la végétation submergée et émergée. L'apport de litière, ponctuel et important au début de l'inondation, a été faible ou inexistant par la suite. Le groupe fonctionnel herbivore–détritivore a atteint un effectif élevé tôt au début de la première année de l'inondation et a maintenu cet effectif pendant une bonne partie de la deuxième année. Par contre, le groupe prédateur–parasite n'a pas progressé de la même façon après l'inondation. Ces changements dans la communauté nectonique après l'inondation ont été provoqués par des modifications de la quantité de litière végétale utilisable comme nourriture et comme habitat. De plus, il est possible que des courants d'eau générés par les vents aient eu un effet sur la distribution du necton pendant l'inondation.

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An important area often neglected in freshwater wetland research has been the study of aquatic macroinvertebrates (Stearns 1978). Although Voigts (1976) and Whitman (1974) provided some data on nektonic invertebrate distribution and abundance in various wetland habitats, little is known of the seasonal variation, the taxa involved, the inherent variability within populations, or the effects of changing habitat conditions. Invertebrates are important to nutrient cycling and detrital processing (Andersson et al. 1988) and provide an important food source for breeding marsh birds (Murkin and Batt 1987). To date, research on wetland invertebrate communities has been hindered by a combination of the absence of background information, the problems associated with quantitative sampling of wetland habitat, and the effort involved in processing quantitative samples (Swanson and Meyer 1973). Increased hydroelectric developments (Newbury et al. 1984) and the development of large controlled impoundments for waterfowl management (Fredrickson and Taylor 1982) have pointed to the lack of information on the effects of flooding on natural ecosystems. The effects of flooding a marsh with established emergent vegetation beds to above-normal levels for prolonged periods are unknown. Whitman (1974) examined the nektonic invertebrate response to reflooding of dry wetland basins following artificial drawdown. He found that the highest

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nekton densities occurred the first year after reflooding as the submersed terrestrial vegetation decomposed and before emergent vegetation became abundant.

The objectives of the present study were to examine the seasonal differences in nektonic macroinvertebrate population levels within and among the dominant cover types of a northern prairie marsh and to determine the response by nekton to prolonged above-normal flooding of marsh habitat.

Methods

Study Area

The study was conducted on the Delta Marsh, a 35 000-ha northern prairie marsh on the south shore of Lake Manitoba in south-central Manitoba (50°11′, 98°19′). Vegetation and physiography of the marsh have been described by Walker (1959, 1965), Anderson and Jones (1976), and Fenton (1970). Experiments were conducted in a series of 5-ha cells created by diking the north edge of the marsh (Murkin et al. 1984). Each cell was equipped with a stop-log water level control structure and an electric pump. The area within each cell was divided into the following five cover types based on the dominant emergent vegetation: open water (standing water with no emergent vegetation), *Phragmites* (*Phragmites australis*), whitetop (*Scolochloa festucacea*), hardstem bulrush (*Scirpus acutus*), and cattail (*Typha* spp.).

Experimental Design

Four of a possible 10 cells (1, 3, 7, and 8) were used in this study. In 1980, all cells were at the same water level as the main body of the Delta Marsh (247.5 m above sea level). In the late fall of 1980, cells 1 and 8 were flooded to 248.4 m to bring them to a depth of approximately 1 m in the naturally occurring cattail stands. These cells remained flooded for the next two sampling seasons (1981 and 1982). In the fall of 1981, cells 3 and 7 were similarly flooded for the remaining year of study (1982).

Pump intakes were screened to exclude fish and macroinvertebrates from the water being pumped into the cells. A series of 7.6-L water samples were taken from all 10 pump discharges once a week from 1 to 30 October 1980. They showed that both fish and macroinvertebrates were effectively eliminated from the pumped water. No attempt was made to monitor eggs or invertebrates smaller than 0.5 mm in the pumped water.

Nekton Sampling Methods

Ten invertebrate sampling sites were randomly established within each of the four experimental cells: two sites within each of five cover types. The sample sites were permanently marked and these same sites were used within and between years. All stations were sampled every 2 wk from 27 April to 27 October each year. Macroinvertebrates were defined as invertebrates retained by a U.S. Standard No. 35 sieve (0.5-mm openings).

To sample the nekton, one activity trap sample was taken at each sample site during each sampling period. The activity trap consisted of a 3.8-L glass jar with a plastic funnel fastened in the jar opening (Whitman 1974). The traps were suspended in midwater column in the morning and retrieved 24 h later (Murkin et al. 1983). Contents of the trap were poured through a No. 35 sieve and the contents of the sieve were then washed into a 500-mL sample bottle. The samples were brought back to the laboratory and sorted live. If fish were present in the sample, they were removed to prevent loss of invertebrates due to feeding by the fish within the sample jar. Fish were found in approximately 5% of the activity trap samples. The effect of fish on activity trap data is discussed in Murkin et al. (1983). Water depth (centimetres) was measured at each site at the time of sampling. Maximum–minimum water temperatures were also determined by placing a thermometer midway in the water column at the activity trap site. A thermometer was placed in the water for 24 h in conjunction with the placement of the activity trap.

Invertebrates were identified only as far as necessary to determine their functional status (Cummins 1974). Due to the overlap of trophic categories suggested by Cummins (1974; also see Thorp and Bergey 1981) and the uncertain taxonomy of wetland invertebrates, only two broad functional groups were used: herbivore–detritivore (H-D) and predator–parasite (P-P). Identification to family was usually sufficient; however, ostracods (Podocopa), copepods (Eucopepoda), and cladocerans (Cladocera) were identified only to order. Chironomidae (Diptera) were identified to subfamily. The invertebrates were sorted by taxa, as indicated, and counted. The number of taxa in each sample was recorded as well as the number of individuals and taxa within each of the two functional groups. The term "diversity" normally refers to the number of species within a sampling unit (Malley and Reynolds 1979); therefore the number of taxa in this study can only be considered a crude index to diversity within the experimental cells. A subsample of each taxon was oven-dried at 105°C for 24 h (Cummins and Wuycheck 1971) to estimate dry weight biomass.

Analyses of the nekton data and water depths followed a split-plot analysis of variance with main effects of flooding and cells within flooding and subplot effects of cover type and time. Log $(x + 1)$ and square root $(x + 1)$ transformations were used where required to stabilize variances. Analyses were conducted on the Vax 11/780 at Utah State University using STATPAK (Hurst 1973). When significant ($P < 0.05$) effects were determined, protected least significant difference tests were used for planned mean comparisons (Carmer and Swanson 1973). Calculations of least significant difference ranges followed Cochran and Cox (1966, p. 305) using weighted t-values (Snedecor and Cochran 1967, p. 116).

Macrophyte Sampling

Standing stems (living and dead combined) of each emergent macrophyte species were recorded during the second week of August each year. A 1-m^2 quadrat was randomly placed within 1 m of the marker stake at each sample site and the number of stems recorded. For submersed plant species, percent cover within the quadrat was estimated.

Results

Macrophytes

Flooding to 1 m above normal had a marked effect on the vegetation within the cells (Table 1). During normal water levels, open-water sites supported dense beds of sago pondweed (*Potamogeton pectinatus*); however, these beds were completely eliminated by flooding. At the invertebrate sampling sites, all emergent vegetation was killed during the first year of flooding. Following flooding, only dead standing litter remained at these sites, and by the second year of flooding, all

TABLE 1. Vegetation characteristics of the invertebrate sampling sites during the second week of August each year, 1980–82.

Vegetation	Cover type	Cells	1980	1981	1982
Submersed[a]	Open water	1 and 8	88.8 ± 10.3[b]	2.5 ± 5.0	0
		3 and 7	93.8 ± 9.5	98.8 ± 2.5	0
	Phragmites	1 and 8	0	0	31.3 ± 47.3
		3 and 7	0	0	1.3 ± 2.5
	Whitetop	1 and 8	0	12.8 ± 24.8	42.5 ± 50.5
		3 and 7	0	0	3.8 ± 7.5
	Bulrush	1 and 8	0	0	0
		3 and 7	0	0	0
	Cattail	1 and 8	0	20.0 ± 24.5	23.8 ± 29.1
		3 and 7	0	0	10.0 ± 20.0
Emergent[c]	*Phragmites*	1 and 8	29.3 ± 7.0	8.8 ± 1.5	0
		3 and 7	30.0 ± 12.0	35.8 ± 13.3	9.8 ± 19.5
	Whitetop	1 and 8	111.5 ± 97.9	0	0
		3 and 7	115.3 ± 61.9	115.8 ± 47.8	0
	Bulrush	1 and 8	90.5 ± 37.5	1.8 ± 3.5	0
		3 and 7	80.0 ± 46.2	101.5 ± 41.7	0
	Cattail	1 and 8	32.0 ± 6.4	0	0
		3 and 7	38.3 ± 18.8	49.3 ± 15.6	6.0 ± 12.0

[a]Percent cover.
[b]x + SD, $n = 2$.
[c]Number of standing stems per square metre.

remaining stems had toppled. During normal water depths, none of the sites, other than open water, had submersed vegetation present. After flooding, *Phragmites*, whitetop, and cattail sites were invaded by bladderwort (*Utricularia vulgaris*). Hardstem bulrush sites had no submersed vegetation before or after flooding.

Nekton Responses

Total invertebrates

Prior to flooding (cells 1 and 8 in 1980, cells 3 and 7 in 1980 and 1981), there were no differences ($P < 0.05$) in nekton abundance and number of taxa among the four experimental cells. In open-water sites, nekton levels increased throughout the spring and summer, reaching yearly maximums ($P < 0.05$) in July and August, followed by a decline into the fall (Fig. 1). *Phragmites* and whitetop sites were dry during these periods. The nekton levels in hardstem bulrush and cattail were very similar prior to flooding. There were peaks in May and June ($P < 0.05$) followed by yearly lows in midsummer with a second peak ($P < 0.05$) in fall. It is interesting to note that the minimum nekton abundance and biomass attained in open-water sites in the spring were similar ($P > 0.05$) to the maximum levels attained in the hardstem bulrush and cattail sites.

During the first year of flooding (Cells 1 and 8 in 1981, cells 3 and 7 in 1982), nekton abundance and biomass increased rapidly in all cover types and, except for total biomass in open-water sites, maintained levels equal to or exceeding the midsummer maximums attained in open water prior to flooding. Biomass was higher ($P < 0.05$) in the *Phragmites* and whitetop sites than in open-water sites early in the flooding period. During the second year of flooding (cells 1 and 8 in 1982), nekton abundance and biomass began at first year flooding levels and, except for whitetop sites, declined through the year to levels similar to those of the preflooding period. In open-water sites there was little change in the number of taxa following flooding. In the other cover types the number of taxa showed flooding responses similar to abundance and biomass.

Functional groups

Comparison between total nektonic invertebrates (Fig. 1) and total H-D indicated that a large portion of the nekton within the experimental cells was in the H-D group. As a result, the H-D abundance and biomass responses are as described for total nekton. The results of the comparison between H-D and P-P in cells 3 and 7 are the same as for cells 1 and 8; therefore for sake of brevity, we present the comparisons from cells 1 and 8 only (Fig. 2).

H-D levels (abundance, biomass, and number of taxa) were generally higher ($P < 0.05$) than P-P levels in open-water sites during most sampling periods prior to flooding (cells 1 and 8 in 1980, cells 3 and 7 in 1980 and 1981) (Fig. 2). In hardstem bulrush and cattail, H-D and P-P levels were similar ($P > 0.05$) throughout much of the period.

Following flooding (cells 1 and 8 in 1981 and 1982, cells 3 and 7 in 1982), H-D abundance was higher than the P-P group during most sampling periods in all five cover types (Fig. 2). This was not true for the biomass comparisons. In open water, hardstem bulrush, and cattail, H-D biomass was higher during most sampling periods until late in the second year of flooding (cells 1 and 8 in 1982) when the biomass of the two groups showed little difference as invertebrate levels in general began to decline. In *Phragmites* and whitetop sites, the H-D and P-P biomasses were very similar during most sampling periods, with H-D biomass being higher during a few isolated sampling periods. The number of H-D taxa was higher during most sampling periods postflooding; however the difference was less pronounced in open water, *Phragmites*, and whitetop during the second year of flooding.

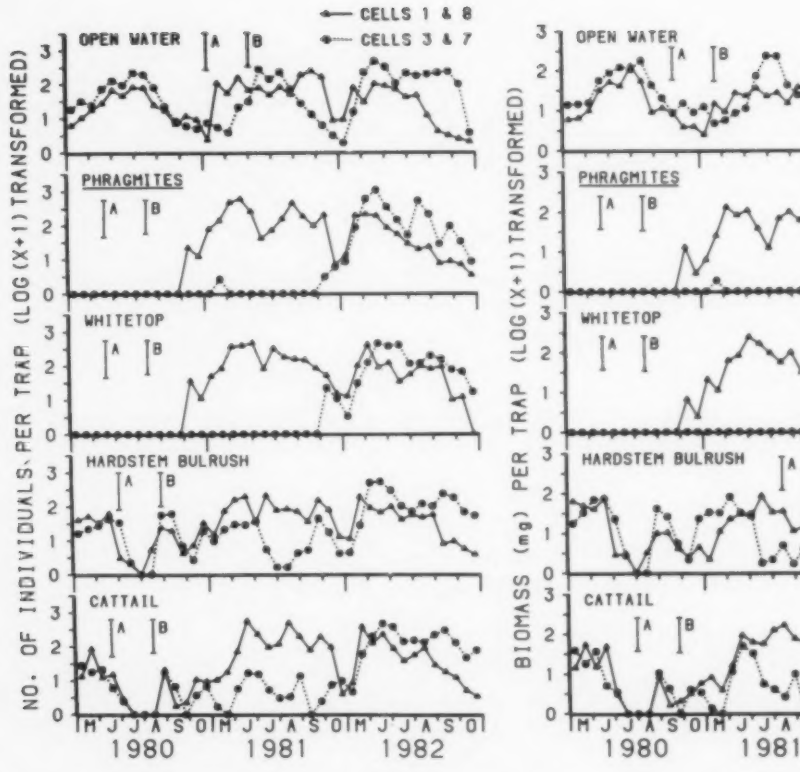
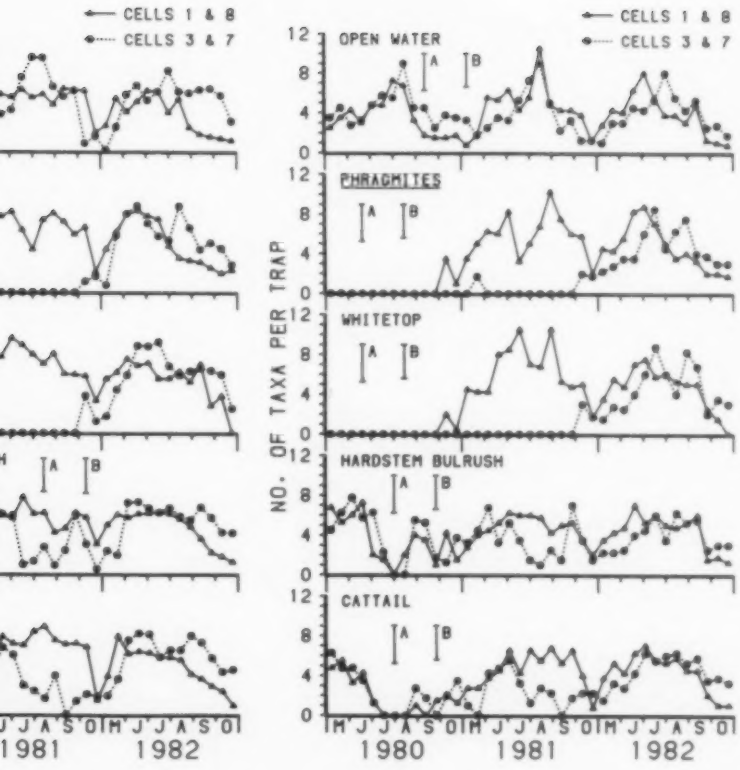


FIG. 1. Total invertebrates (all taxa combined) in activity traps. *A* = least significant differ
versus cells 3 and 7) within a sampling period. Values for *A*: density = 1.04, biomass = 0.81,
flooding schedule over time. Values for *B*: density = 0.99, biomass = 0.87, number of taxa
schedule by sampling period (not indicated on figure) density = 1.05, biomass = 0.94, numb



t difference (LSD) range ($P < 0.05$) for comparison of flooding schedules (cells 1 and 8 0.81, number of taxa = 3.70. B = LSD range ($P < 0.05$) for comparison within a f taxa = 3.40. LSD range ($P < 0.05$) for comparison among cover types within a flooding , number of taxa = 3.68.

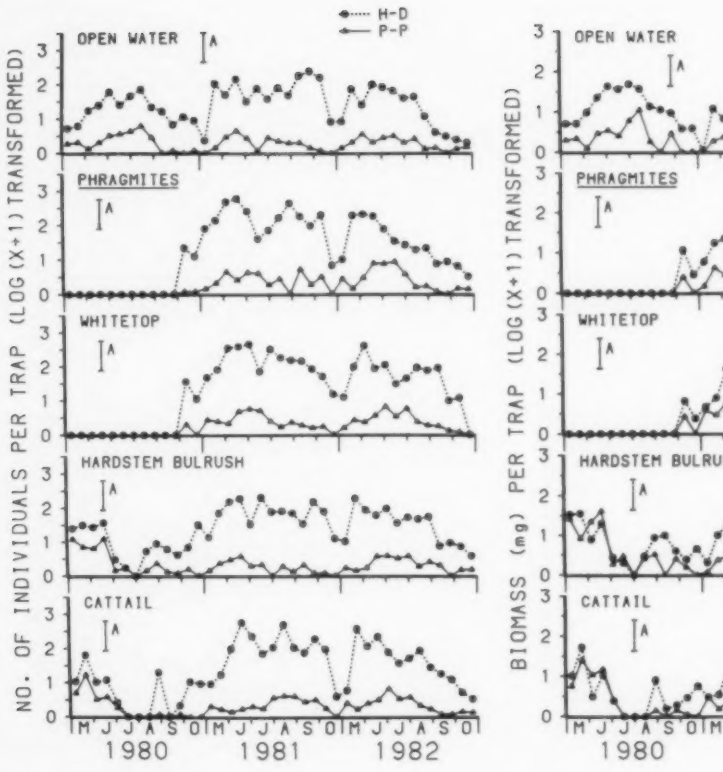
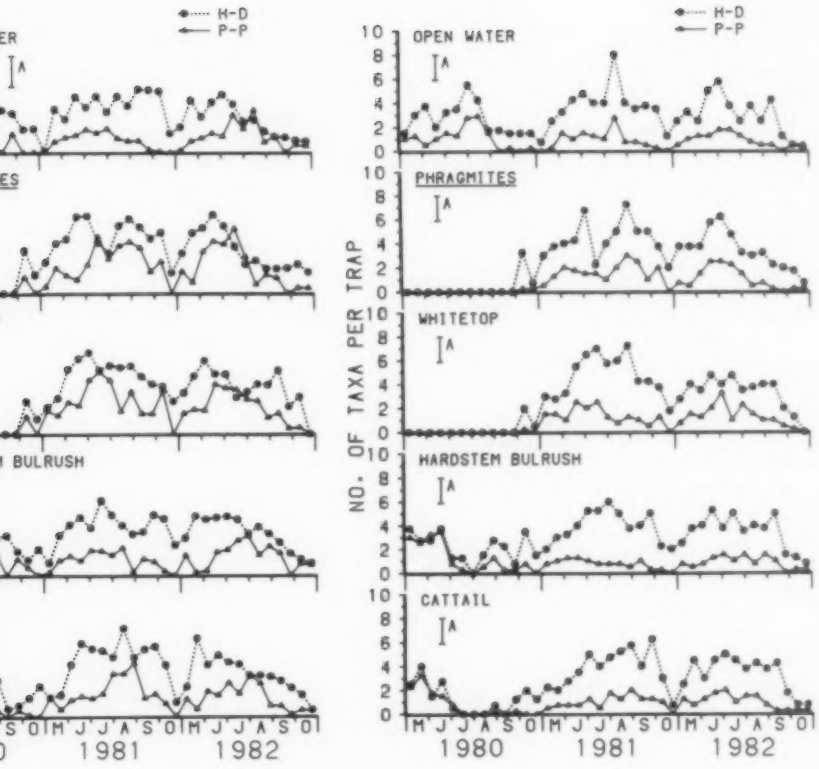


FIG. 2. Comparison of herbivore–detritivore and predator–parasite functional groups
comparison between the two functional groups within a sampling period. Values for



l groups in activity traps, cells 1 and 8. *A* = least significant difference (LSD) range ($P < 0.05$) for
lues for *A*: density = 0.86, biomass = 0.76, number of taxa = 2.09.

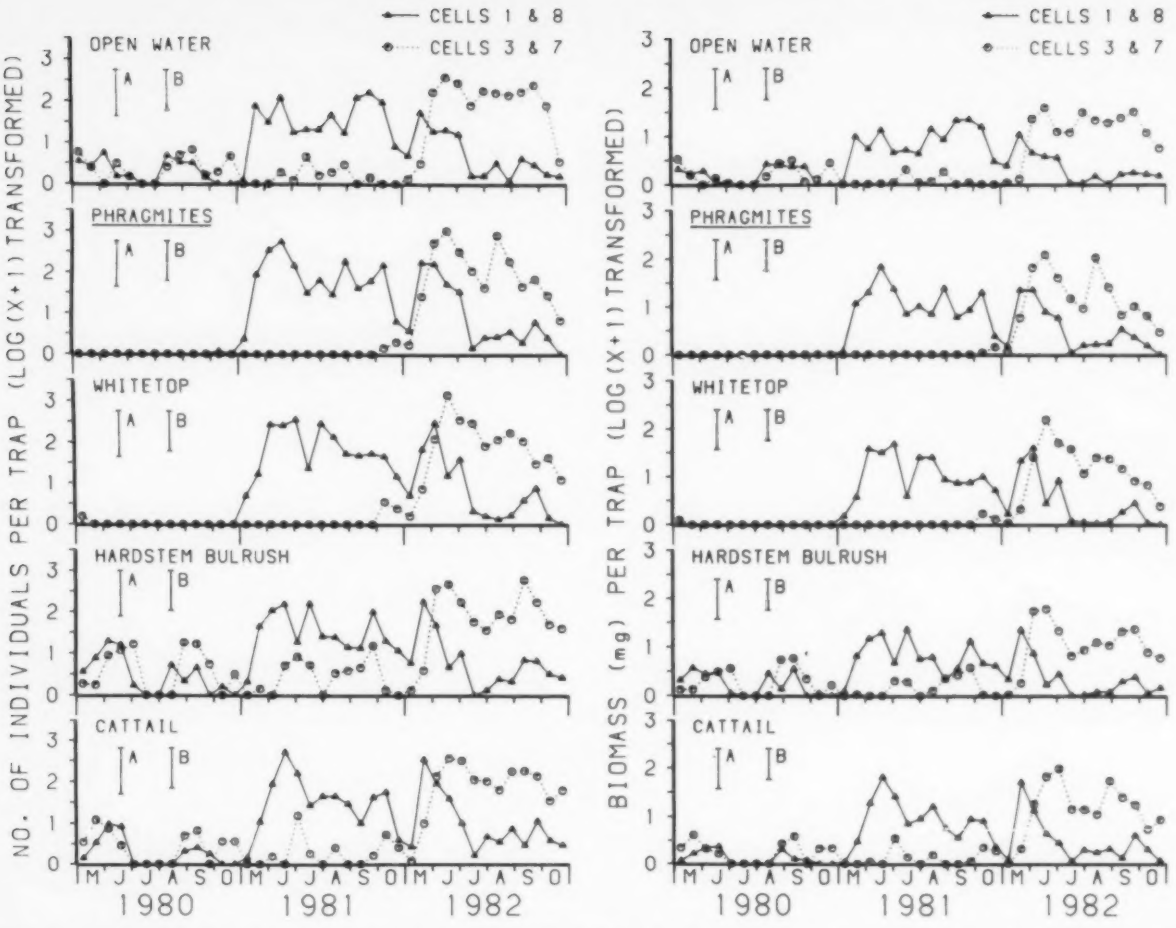


FIG. 3. Cladocerans in activity traps. A = least significant difference (LSD) range ($P < 0.05$) for comparison of flooding schedules (cells 1 and 8 versus cells 3 and 7) within a sampling period. Values for A: density = 1.11, biomass = 0.83. B = LSD range ($P < 0.05$) for comparison within a flooding schedule over time. Values for B: density = 0.97, biomass = 0.64. LSD range ($P < 0.05$) for comparison among cover types within a flooding schedule by sampling period (not indicated on figure) density = 1.04, biomass = 0.67.

Individual taxa

Cladocerans — Prior to flooding (cells 1 and 8 in 1980, cells 3 and 7 in 1980 and 1981), cladoceran abundance and biomass were highest in open water, hardstem bulrush, and cattail sites during the spring and fall, with very low levels recorded during the midsummer periods (Fig. 3). Abundance and biomass were similar among the three cover types with standing water.

Following flooding, cladoceran abundance and biomass increased ($P < 0.05$) in all cover types to levels well above those found prior to flooding (Fig. 3). Levels remained high through the first year of flooding (cells 1 and 8 in 1981, cells 3 and 7 in 1982) and then abruptly declined ($P < 0.05$) to very low levels midway through the second year of flooding (cells 1 and 8 in 1982). This response was very similar in all five cover types. Fall levels during the second year of flooding were similar to fall levels prior to flooding.

Hyalella azteca — Prior to flooding (cells 1 and 8 in 1980, cells 3 and 7 in 1980 and 1981), *Hyalella azteca* (Amphipoda) abundance and biomass attained prolonged summer peaks in open-water sites (Fig. 4). In hardstem bulrush and cattail, *H. azteca* declined from spring levels similar to open-water sites to very low (almost nonexistent) levels in midsummer. It then reappeared in late summer/early fall at levels similar to open-water sites in the fall.

During the first year of flooding (cells 1 and 8 in 1981, cells 3 and 7 in 1982), abundance and biomass in open-water sites reached relatively stable levels that were below the midsummer peaks prior to flooding (Fig. 4). Levels declined during the latter half of the second year of flooding (cells 1 and 8 in 1982). In the other four cover types with emergent vegetation, *H. azteca* abundance and biomass increased slowly during the first year of flooding, not reaching maximum levels until late summer or fall. These levels were then maintained through much of the second year of flooding.

Discussion

Environmental Changes

Physical factors, such as water temperatures, water depths, and water movements, affect invertebrates both directly through their influence on growth and reproduction and indirectly

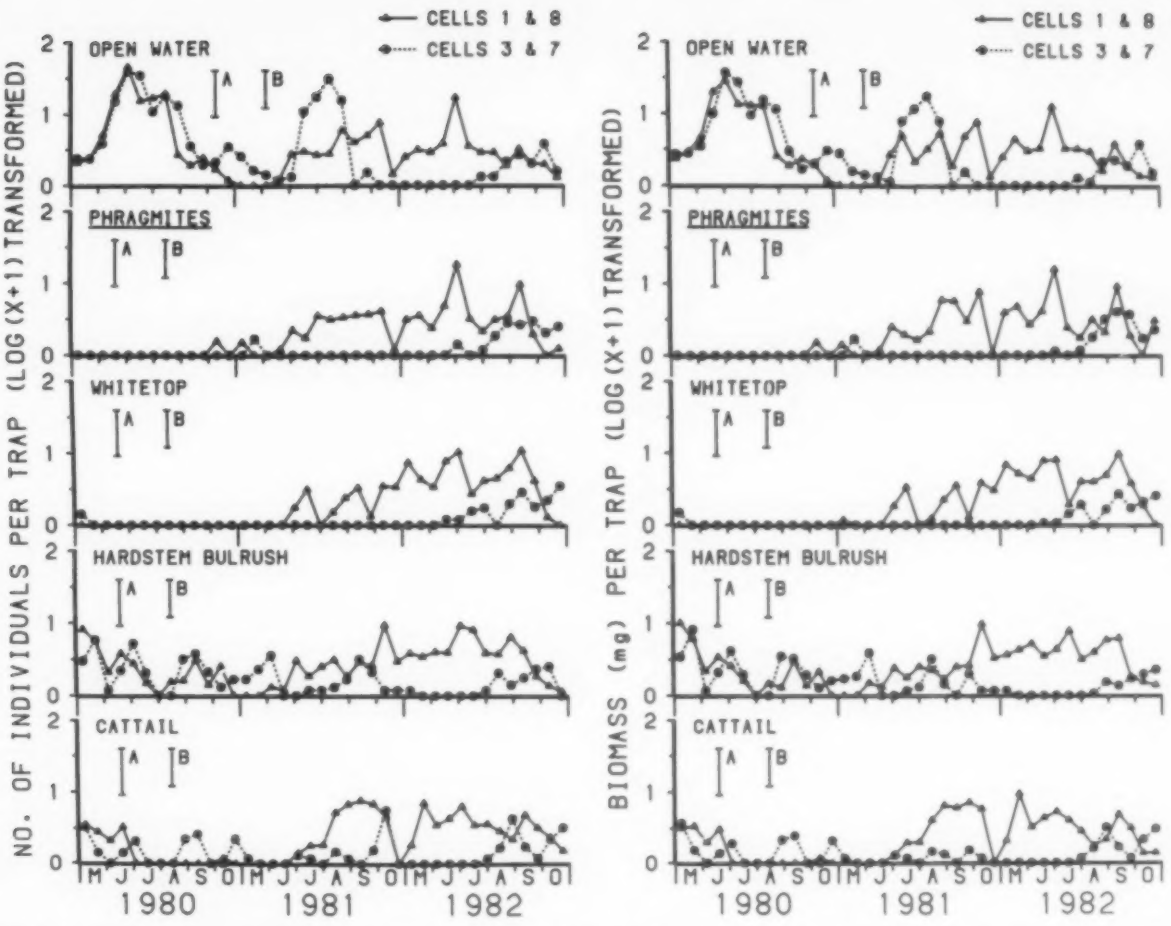


FIG. 4. *Hyalella azteca* (Amphipoda) in activity traps. *A* = least significant difference (LSD) range ($P < 0.05$) for comparison of flooding schedules (cells 1 and 8 versus cells 3 and 7) within a sampling period. Values for *A*: density = 0.64, biomass = 0.64. *B* = LSD range ($P < 0.05$) for comparison within a flooding schedule over time. Values for *B*: density = 0.52, biomass = 0.52. LSD range ($P < 0.05$) for comparison among cover types within a flooding schedule by sampling period (not indicated on figure) density = 0.53, biomass = 0.53.

through impacts on litter production and processing. Environmental temperatures affect invertebrate growth rates and reproduction (Wiederholm et al. 1977; Vijverberg 1980) as well as decomposition rates of wetland vegetation (Godshalk and Wetzel 1978). In this study, both water and substrate temperatures varied within a year; however, flooding to 1 m above normal appears to have had little effect on the water temperatures within the experimental cells. Although flooding eliminated the standing emergent vegetation and its shading effect, it appears that the increased water volumes and wind-induced mixing, due to loss of the sheltering effect of the vegetation, resulted in water temperatures very similar to the periods of normal water depths.

Mixing by wind appears to be important even during periods of normal water depths. During these periods, there were no differences in water temperatures among cover types even though the substrate and/or submersed vegetation in open-water sites were exposed to direct sunlight for much of the year, while the water surfaces in emergent vegetation beds like cattail were shaded throughout the year. This wind-induced mixing may be an important feature of wetlands throughout the northern prairie environment. In this study, it appears that while water and substrate temperatures may have affected invertebrate levels and litter processing between seasons within a year, there were little or no effects of temperature among cover types or between normal and above-normal water depths.

Macrophytes

There are two important components of the emergent plant litter in marshes: the standing litter and the fallen litter (Davis and van der Valk 1978a). Following senescence, the standing dead plants form the standing litter compartment. It becomes fallen litter when it enters the water column through fragmentation of leaves and stems or toppling of the entire plant. Once litter enters the water, it becomes available to aquatic invertebrates. During periods of normal water depths, northern prairie marshes experience two main periods of fallen litter input. During the fall following senescence, there is some fragmentation and toppling of stems. This fall input is minor compared with that during the following spring (Davis and van der Valk 1978b). Winter and spring storms cause extensive fragmenta-

tion of standing litter; therefore, fallen litter input to the water column is high at the time of spring thaw (Davis and van der Valk 1978a).

Besides the initial litter input, the processing and movement of detritus within the wetland may be important in determining the succession and location of nektonic invertebrate groups within the system (Nelson and Kadlec 1984). Although processing of litter and the various strategies and functional status of the invertebrate groups involved are becoming known for streams (Cummins 1974; Vannote et al. 1980), they are poorly understood in wetlands. Within lakes, the movement of macrophyte litter from vegetation beds to open water is important to the secondary productivity of open-water areas (Howard-Williams and Lenton 1975; Wetzel 1983, p. 704). There have been no studies of detrital transport within freshwater wetlands. Polunin (1982) has documented the importance of the detritus of emergent vegetation to the productivity of open-water areas in a small fenland pond.

A major impact of the flooding to 1 m above the cattail beds within the experimental cells was on the existing vegetation (Table 1). This, in turn, affected both the litter input and future litter production. All existing emergent vegetation at the invertebrate sampling sites was killed by the high water levels. Consequently, there was no new production of emergent litter at these sites following flooding. Much of the existing standing litter was submersed by the high water levels and was therefore forced directly into the fallen litter compartment, although the stems remained standing. All the standing litter in whitetop sites was completely submersed by the flooding. In hardstem bulrush sites, there was some standing litter during the fall when the cells were first flooded, but by the following spring, no standing litter remained above the water surface. Most of the *Phragmites* and cattail standing litter was covered by the high water levels, although some stems remained above the surface at a few of the sampling sites into the second year of flooding. In open-water sites, the sago pondweed beds present during periods of normal water depths were completely eliminated by the high water levels. In summary, the flooding to 1 m above normal resulted in a single large input of litter at the time of flooding with no new litter production during flooding except in some of the *Phragmites*, whitetop, and cattail sites that were invaded by bladderwort during the second year of flooding (Table 1).

Nekton

Total invertebrates

The spring and fall maxima of total nektonic invertebrates in cattail and hardstem bulrush (Fig. 1) coincided with the predicted periods of maximum emergent litter input to the water column. The difference in habitat structure between open-water sites and emergent vegetation with fallen litter and standing stems, however, did not result in different nekton levels between the two areas during the spring and fall of periods with normal water depths. Apparently, some factor other than litter input or habitat structure limits nekton levels during these periods. The growth and reproduction of invertebrates are affected by temperature, and the low temperatures may be limiting nektonic invertebrate levels during the spring and fall.

Nekton levels during periods of normal water depths differed among cover types and over time. These differences appear to be related to water temperatures, litter input, and habitat structure. Results of this study agree closely with the nekton levels reported by Voigts (1976). Although he sampled in June only, he found maximum nekton levels in open-water sites with submersed vegetation and lowest levels in stands of emergent vegetation. He suggested that maximum nekton levels would occur in areas with emergent vegetation intermixed with submersed vegetation because these areas provide maximum cover for nektonic invertebrates. Besides cover, these areas may benefit from litter input to the open-water sites from adjacent emergent vegetation beds (Polunin 1982; Nelson and Kadlec 1984) as well as the litter production and habitat structure provided by the submersed vegetation.

In response to the litter input and changes in habitat structure at the time of flooding, nekton levels (density, biomass, and number of taxa) increased in all cover types (Fig. 1). Besides litter input, another important effect of flooding was the removal of the sheltering effects of the emergent vegetation beds. Once these beds were gone, wind-induced water currents may have become a dominant factor affecting nekton distributions. By the second year of flooding, emergent vegetation beds were almost completely eliminated (Table 1), and during this time, little difference in nekton levels (density, biomass, and number of taxa) was found among the five cover types.

Nekton levels declined during the spring and fall of both years of flooding, possibly due to the low water temperatures during these periods, as discussed earlier. Some taxonomic groups may overwinter as eggs or in other forms that were not sampled by the techniques used in this study.

Functional groups

During the spring and fall of periods with normal water depths, the P-P levels were higher in the emergent vegetation compared with open-water sites, not only in absolute densities, biomass, and number of taxa (Fig. 2), but also relative to H-D levels. This would indicate that the P-P are not simply responding to the H-D levels within the two habitat types. The structural component of the environment in emergent vegetation beds may be important to the P-P group, as suggested by Street and Titmus (1982) and Andersson and Danell (1982). The standing litter may be important to predators that stalk or ambush prey from concealed perches. This structural component is not available in open-water sites in the spring. As an example, predaceous dytiscid beetles were one of the dominant predators found in this study. Merritt and Cummins (1984, p. 428) have termed dytiscid larvae as "climbers," suggesting that a rigid structural component may be an important feature of their habitat.

In open-water sites, the P-P levels increased in midsummer, possibly due to the greater availability of prey. Another important factor may be the greater structural complexity of the open-water sites due to the presence of the submersed vegetation. It is interesting to note that the maximum P-P levels in the open-water sites were similar to the P-P levels in emergent vegetation (Fig. 2) during the spring. This suggests that the structural component may be even more important to P-P than the H-D (prey) levels. Throughout the summer, P-P levels remained significantly lower than H-D levels (Fig. 2). Hall et al. (1970) also found in small fish ponds with no emergent vegetation that predator levels remained well below prey levels even when prey levels increased during the summer. In their study, they also found that invertebrate predators had no effect on invertebrate prey standing crop or productivity.

The P-P group did not show the pronounced changes due to flooding that the H-D group did. There were no substantial increases in P-P levels following flooding in spite of increases

in H-D (prey) levels. In some cases, for example hardstem bulrush sites, P-P levels actually decreased following flooding. This indicates that some factor other than prey levels, possibly habitat structure (Street and Titmus 1982), may limit the P-P groups. The loss of habitat structure and complexity in hardstem bulrush sites through rapid decomposition of the fallen and standing litter may have made the habitat less suitable for predaceous invertebrates.

Nektonic invertebrates, responding directly to the submersed litter as a food resource and as habitat structure, would be affected by the amount of litter present within the water column. As discussed earlier, the amount of available litter would decline throughout the period of flooding. Given the decomposition rates of the species of emergent vegetation in this study, there would be much less litter left by the end of the second year compared with the initial input. If the H-D group is affected by the amount of litter in the system, H-D levels would be expected to be higher during the first year of flooding and then decline through the second year of flooding. This seems to be the case within the experimental cells (Fig. 2), except that the development of submersed vegetation beds in some of the shallower sites during the second year of flooding may have allowed H-D levels to remain high at these sites through the second year.

Individual taxa

Cladocerans — Within the H-D group, cladocerans declined to very low levels in all cover types during the summer (Fig. 3). Voigts (1976) also found that cladoceran levels decreased as submersed vegetation increased. Decline in cladoceran levels during midsummer has been commonly observed in shallow lakes; yet in most cases, no precise cause has been determined (Prepas and Rigler 1978). Some authors have suggested predation as the main reason for reduced cladoceran populations in midsummer (Whiteside et al. 1978; Threlkeld 1979). In this study, P-P levels increased during midsummer, but whether they affected cladoceran levels cannot be determined.

The cladoceran group was an important component of the H-D response during the first year of flooding (Fig. 3). Cladoceran levels remained high through the first year of flooding and did not show the midsummer decline as during periods of normal water depths. By the second year of flooding, however, cladoceran levels began to decline. Cladocerans may not be responding directly to the fallen or particulate litter as a food resource because they are generally considered to feed on phytoplankton (Porter 1977; Porter and Orcutt 1980) and, in some cases, bacteria within the water column (Coveney et al. 1977). The most common species of cladocerans recorded in the Delta Marsh are within the planktivore group (Smith 1968). In some systems, cladocerans are considered the principle consumers of primary production (Hebert 1978). They cannot only select algae and bacteria from a mixture of fine particles within the water column, but they have been shown to select individual species of algae from mixtures of phytoplankton (Porter and Orcutt 1980). Dense populations of cladocerans are potentially able to graze more than 100% of the daily phytoplankton production (Porter 1977). Phytoplankton levels within the experimental cells during the first year of flooding were actually lower than during periods of normal water depths (Hosseini 1986), possibly due to the grazing effects of the high cladoceran levels. Phytoplankton levels did decrease during the second year of flooding (Hosseini 1986), as did cladoceran levels. The phytoplankton production may have declined to a point where they could no longer support the cladoceran densities found early in flooding.

Hyalella azteca — An important component of the summer peaks of nekton during periods of normal water depth was *H. azteca* (Fig. 4). *Hyalella azteca* are generally considered detritivores (de March 1981, p. 64), feeding primarily on epiphytic and epibenthic algae associated with particulate litter (Hargrave 1970a). They ingest fine detrital particles and digest the algae and bacteria within the litter (Hargrave 1970b). The litter deposited in emergent vegetation beds may be transported to areas of open water, especially once it is reduced to fine particle size (Polunin 1982; Nelson and Kadlec 1984). Polunin (1982) showed that input of fine organic detritus to open-water sites was highest during the summer, and much of the deposited material originated from the surrounding reed beds. With increasing water temperatures in early summer, *H. azteca* may be able to take advantage of this input of fine litter particles to the open-water sites. These sites supported dense beds of sago pondweed during the summer of periods with normal water depths. Turnover of the submersed vegetation will provide litter input, especially in late summer/early fall as the beds senesce (Smock and Stoneburner 1980). Voigts (1976) found maximum *H. azteca* levels in areas with dense vegetation and suggested that the shelter provided by the vegetation is important to *H. azteca* use of these areas.

Hyalella azteca also did not respond immediately to flooding. *Hyalella azteca* levels did not increase until July of the first year of flooding even though water temperatures were suitable for growth and reproduction earlier in the year (de March 1977). This delay may be due to the fact that *H. azteca* may prefer litter somewhat finer than the large litter particles (leaves and stems) introduced by the initial flooding. It may have taken until midsummer for the litter to be processed to a point that it was suitable to *H. azteca*. Throughout the last half of the first year of flooding, *H. azteca* levels increased, possibly in response to the availability of the appropriate size and quality of litter. Peaks occurred during the second year of flooding when most of the original litter would have been processed to a fine state. There was no difference in *H. azteca* among the five cover types during the second year of flooding, possibly due to the wind-induced mixing described earlier. Throughout flooding, *H. azteca* levels were lower than during the summer in open-water sites when submersed vegetation was abundant. This suggests that submersed vegetation provides food and shelter important to *H. azteca* growth, reproduction, and survival.

In conclusion, it appears that the amount and quality of the various detrital components available as both food and habitat affect the distribution and abundance of nektonic invertebrates in wetland systems. In addition, nekton distributions appear to be greatly affected by wind-induced water currents. Mixing by these currents resulted in no differences across the five cover types during the second year of flooding. This mixing would not only affect the invertebrates within the water column directly but also the detrital resources upon which the nekton depends for food and habitat.

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Multivariate Description of Pacific Herring (*Clupea harengus pallasi*) Stocks from Size and Age Information

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Fisheries management must trade off biological conciseness with institutional and practical constraints, which may preclude separate management of all genetic stock units but should ensure long-term survival of such components in each area. The technique described here, while unable to explicitly identify genetic differences, is applicable to other species and would be particularly valuable for preliminary studies where limited resources preclude the use of expensive and analytically more complex techniques such as morphometric and meristic or electrophoretic analyses which are more suitable for that task. The method developed in this study involves the application of discriminant function and canonical variates analysis to information on size and age structure of Pacific herring (*Clupea harengus pallasi*) from samples representing the seven major migratory populations and other spawning aggregations in six geographical regions of coastal British Columbia. Results of the analysis quantify the separation of stocks of herring between geographical regions, and at a finer spatial scale, within all regions. Generally, one or more migratory stocks occurred together with minor stocks in each geographical region.

La gestion des pêches doit concilier la concision biologique d'une part, et les contraintes institutionnelles et pratiques d'autre part, ce qui pourrait empêcher une gestion séparée de toutes les unités de reproducteurs, mais devrait assurer leur survie à long terme dans chaque région. La technique décrite ici, quoique ne permettant pas d'identifier explicitement les différences génétiques, est applicable à d'autres espèces et serait particulièrement utile dans les études préliminaires où les ressources limitées interdisent l'utilisation de techniques coûteuses et analytiquement plus complexes comme les analyses morphométriques et méristiques ou électrophorétiques qui conviennent mieux à cette fin. La méthode mise au point dans la présente étude consiste à appliquer l'analyse par fonction discriminante et par variables canoniques à de l'information sur la répartition des tailles et des âges du hareng du Pacifique (*Clupea harengus pallasi*) provenant d'échantillons représentant les sept grandes populations migratoires et d'autres concentrations de frai dans six régions géographiques du littoral de la Colombie-Britannique. Les résultats de l'analyse quantifient la répartition des populations de harengs entre les régions géographiques et, à une échelle spatiale plus fine, à l'intérieur de chaque région. En général, une ou plusieurs populations migratoires se retrouvent avec des populations plus faibles dans chaque région.

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The definition of genetically discrete stocks of fish is perhaps the most important and difficult component of any fisheries management scheme. The dilemma from both a biological and a management perspective is how to determine the correct spatial scale to employ in identifying stocks of fish (Larkin 1981). In the absence of detailed genetic information, how far should one amalgamate possibly distinct stock units, given the risk that any exploitation rate will differentially impact the least productive, yet genetically unique, stocks. The common solution is to collect samples from the major fishing or spawning areas and evaluate any differences which may imply genetically distinct stocks of fish which should be managed individually. The techniques used to describe these stocks range from simple qualitative methods like tagging or marking to fairly complex quantitative procedures like morphometrics or genetic analysis. Unfortunately, the spatial resolution of current stock identification procedures appears to relate inversely to their complexity and tends to preclude genetic evaluation of stock differences at the spatial scale required for rational fishery management.

Stock identification of Pacific herring (*Clupea harengus pallasi*) has been attempted with many techniques, beginning with morphometric and meristic data (Tester 1937a, 1937b, 1949), augmented by a long-term tagging study (Stevenson 1954). These data, combined with information on the location and timing of spawning (Haegele and Schweigert 1985; Hay and Kronlund 1987), provided a qualitative description of what were inferred to be genetically discrete stocks and formed the basis of the current stock concept for British Columbia herring. Although these studies indicate differences among herring from different areas in a variety of characters, there is also evidence from tagging that the separation is not exact and that a significant amount of intermixing occurs between geographically adjacent areas. Because the current roe fisheries occur on individual spawning beds, it is important to be able to delineate distinct stocks of fish on a relatively fine spatial scale, which has not been possible with any of the foregoing techniques.

In this study, I used multivariate techniques to analyze information on the size at age and the age structure of herring samples from geographically separated spawning beds. The objective was to provide some additional insights into the probable stock

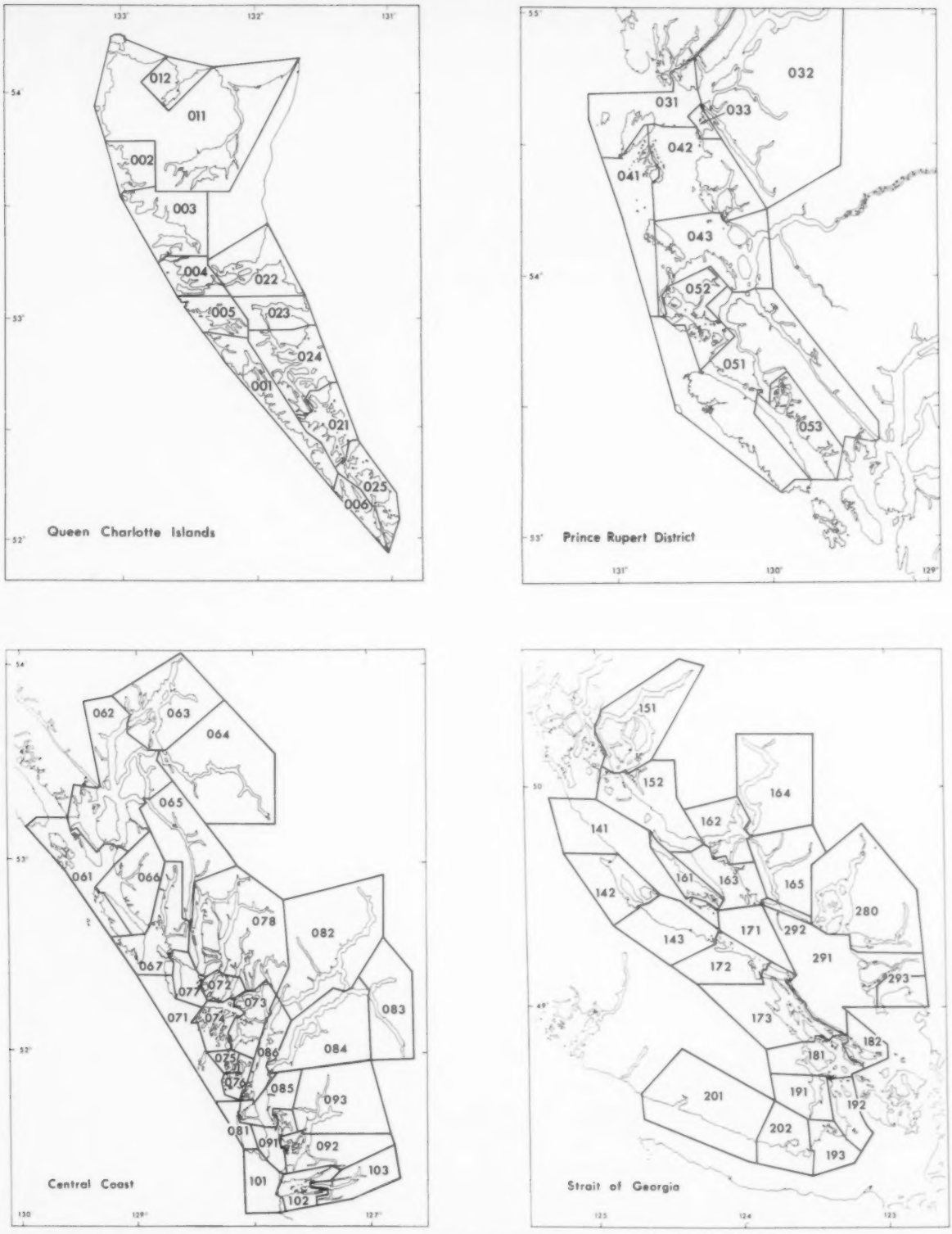
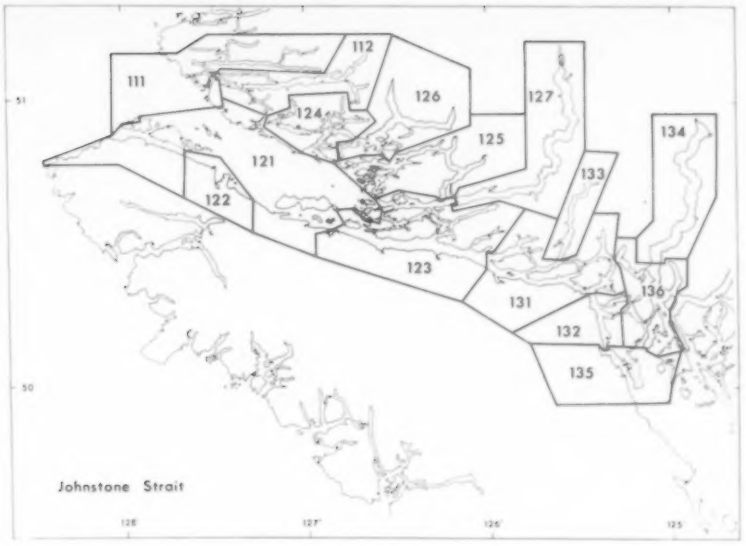


FIG. 1. Sections within the six geographical regions of coastal British Columbia delineating the seven assessment regions (defined in Table 1) used for stock assessment and management of the roe fishery. (*Fig. 1 continued next page*)



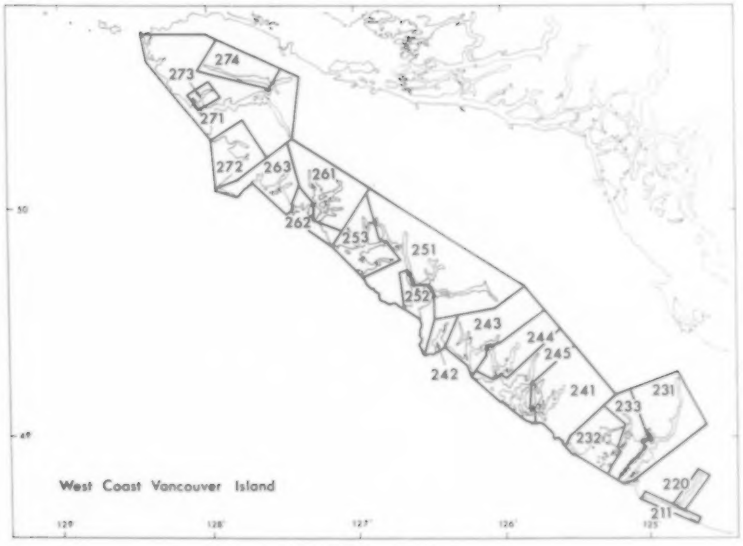


FIG. 1. (*Concluded*)

structure of herring populations within British Columbia and to identify any distinct stocks within our currently recognized assessment regions which should be managed separately. The results support the stock concept currently in use for most assessment regions except for the Strait of Georgia. In addition, some of the suspected differences suggested by earlier tagging and morphometric studies are quantified.

Methods

The biological sampling data for British Columbia herring are identified with a specific geographical locality within a spatial unit known as a section. Sections contain aggregates of geographically separated spawning beaches. A number of sections may constitute one of the seven major herring populations or stocks currently recognized for annual assessment and fishery management (Haist and Rosenfeld 1988). The seven populations are contained within five of the six geographical regions of coastal British Columbia (Fig. 1). Uncertainty exists about the relative discreteness of northern and southern populations in the Strait of Georgia and the west coast of Vancouver Island. Johnstone Strait and a number of the mainland inlets appears to support numerous minor stocks which are apparently distinct from the major populations (Taylor 1964).

Sample Selection

The samples of herring chosen for this analysis were all taken by seine gear within 1–2 wk of spawning. It is assumed that

TABLE 1. Geographical affiliations of Pacific herring spawning areas in relation to stock assessment units, and sections for sampling data in 1975, 1980, and 1981.

Stock assessment region	Spawning area	Section Nos.	Plotting symbols for Fig. 3–7
Queen Charlotte Islands	Louscoone Inlet	6	1
	Skincuttle Inlet	21, 25	3
	Cumshewa Inlet, Laskeek Bay	23, 24	4
	Area 2W[a]	1–5	2
	Skidegate Inlet[a]	22	5
Prince Rupert District	Chatham Sound	31, 33, 42	1
	Porcher Island	43, 52	2
	Portland Canal[a]	32	3
Central Coast	Kitasu Bay	67	1
	Seaforth Channel	72, 74, 78	2
	Kildidt Sound	75, 76	3
	Kwakshua Channel	85, 86, 91	4
	Mainland Inlets[a]	63, 64, 82, 84, 92, 93, 102, 103	5
Strait of Georgia, south	Gulf Islands	173, 181, 182, 192	5
Strait of Georgia, north	Lambert Channel	141–143	2
	Powell River	152	3
	Nanoose Bay	172	4
	Deepwater Bay	132	6
	Jervis Inlet[a]	163, 164	7
	Johnstone Strait[a]	111–136, excluding 132	1
West coast Vancouver Island, south	Barkley Sound	231–233	1
	Clayoquot Sound	241–245	2
West coast Vancouver Island, north	Nootka Sound	251, 252	3
	Esperanza Inlet	253	4
	Kyuquot Sound[a]	261–263	5
	Quatsino Sound[a]	271–274	6

[a]Spawning areas which represent minor stocks and are not part of the stock assessment region.

fish would be at or very near to their final spawning destination. However, there are indications from recent in-season tagging in some areas that fish may still be as far as 30 km from their spawning destination at this time. It is unlikely that this would seriously affect results in general but could make the separation of spawning areas within some regions less clear than if all samples were taken right on the spawning beds. The samples used in this study consisted of fish taken either in the commercial fishery, in pre-roe fishery charter vessels, or in conjunction with tagging or other research programs. No gillnet samples were used due to the bias in the size selection of the fish in the samples. Because of their proximity to peak ripeness and spawning, I assumed that there would be no bias due to differential growth effects between regions.

The three years of data chosen for the analysis included those with the greatest number of samples from the greatest variety of spawning areas on the British Columbia coast. Three years were chosen to hopefully provide evidence for similar and consistent aggregation of samples into distinct stocks. For each year the samples were aggregated into each of the five main geographical regions of the British Columbia coast encompassing the seven currently recognized stock assessment regions. Johnstone Strait is included with the Strait of Georgia in this analysis because it includes numerous spawning areas which have unknown relationships with those in the Strait of Georgia. Herring migrate from offshore feeding areas to spawn in the Strait of Georgia via Johnstone and Juan de Fuca straits and could intermix with fish spawning in these areas. Within each geographical region the samples were subdivided into discrete spawning areas or beds representing both the major migratory stocks harvested by the roe fishery and the minor often nonmigratory stocks (Table 1; Fig. 1).

Statistical Analysis

The data for the analysis consisted of samples of about 100 fish for each of which the length, weight, and age were determined. I calculated the mean lengths and weights at each age and determined the proportion of each age class in the sample. To make the sample comparisons consistent between spawning areas, only those with complete information for age classes 3–6 were retained for further analysis. These age groups accounted for more than 90% of the fish for almost all of the samples. Ordination analyses were performed to attempt to define discrete groupings of samples. Analyses wre performed with the Statistical Analysis System routines (SAS 1988). Prior to any of the ordination analyses the raw data were plotted to examine their distributions (Fig. 2) and tested for normality using the Shapiro–Wilk statistic. The distributions of most of the mean lengths and weights at age were normal, while a number of the proportion at age estimates differed significantly from normality.

Discriminant Analysis

Discriminant function analysis is a technique which is frequently used to assess multivariate differences among data sets which are assumed to represent separate groups of objects (Pimentel 1979; Lachenbruch 1975; Tatsuoka 1971). The major

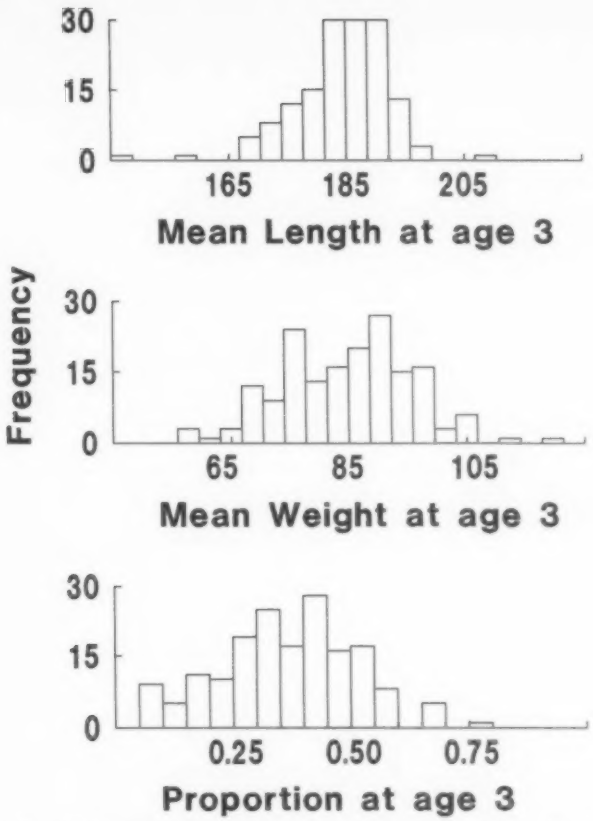


FIG. 2. Frequency distribution of the mean length, weight, and proportion of fish at age 3 for the samples from the Strait of Georgia in 1975.

assumption, as with all multivariate techniques, is that the data follow a multivariate normal distribution and are homoscedastic. For data which are not normally distributed, it is possible to use a number of nonparametric techniques that rely on nearest neighbour distance measures or kernel density estimation procedures to define group membership. Because some of the data appeared not to be normal, I ran a number of comparisons of parametric and nonparametric discriminant analyses. They produced essentially the same results, although for the nonparametric methods the results were quite sensitive to the choice of the number of nearest neighbours or the size and shape of the radius for the kernel estimator. Hence, for consistency, I have used the parametric discriminant function analysis procedure throughout.

Discriminant analysis and crossvalidation were used to assess the discreteness of the samples from all the spawning areas within the five geographical regions representing the seven herring populations in each year. Subsequently, the analysis was repeated for geographically discrete spawning beds within each geographical region. Jackknifed classification error rates were calculated by omitting each sample one at a time and fitting the discriminant function. The function was then used to classify the omitted sample. Because of the small sample sizes representing some of the smaller spawning beds for minor stocks, a pooled covariance matrix is assumed for all analyses. Canonical discriminant analysis was used to assess statistical differences in Mahalanobis distances (D^2) between pairs of geographical regions and spawning areas within regions. This procedure was also used to ordinate the data in a two-dimensional space along the first two canonical axes.

Results

British Columbia Coast

The percentage classification accuracy based on a crossvalidated discriminant function analysis ranged from 60 to 92% for the five geographical regions (Table 2). With five regions the random placement of samples into regions would yield an expected 20% accurate classification rate. The results in Table 2 indicate that the discriminant functions are able to account for a significant amount of the differentiation of samples between regions. Mahalanobis distances between the centroids of each pair of regions were compared with an F-statistic and found to be significantly different in all years. This indicates that there is a readily detectable differentiation among fish from these five regions. Misclassification of samples between regions was generally to the geographically adjacent region. In particular, misclassification of samples from the southern regions to the northern regions was rare and vice versa.

Queen Charlotte Islands

Discriminant function analysis results for the five geographically discrete spawning areas within this region are not as striking (Table 3). Classification success of samples to their area of origin ranged from 50 to 100% where four or more samples were available. Samples were identified to area of origin with much better than random success for all five areas in all years. Results were best for Area 2W and Skidegate Inlet followed closely by Skincuttle and Cumshewa inlets. Misclassification results suggest a clear separation of fish from Skidegate Inlet and the other four areas. Area 2W fish are distinct from Skincuttle and Cumshewa inlets but appear to overlap with Louscoone Inlet in some years. Similarly, Skincuttle Inlet is distinct from Louscoone and Cumshewa inlets in some years and overlaps with them in others. These results are supported by the significant F-statistics for Mahalanobis distances among spawning areas in most cases where available.

Plots of the first two canonical variates show clear separation of Area 2W and Skidegate Inlet fish from the other three stocks in 1975 (Fig. 3). A similar pattern is evident in 1980 and 1981 although the separations are not nearly as pronounced. The samples from Louscoone Inlet are intermediate between the fish from Skincuttle and Cumshewa inlets and those from Area 2W. Hence, the data suggest that distinct stocks of fish may exist in Area 2W and Skidegate Inlet, and while there is some evidence for separation of the other three spawning areas, it is variable enough to make their practical management as separate entities difficult if not impossible.

Prince Rupert District

Classification accuracy for the three spawning areas within this region ranged between 29 and 86% (Table 3). Classification success was greatest for Portland Canal samples in 1975, while it was less than random for Chatham Sound samples in 1980 and 1981. Misclassifications were primarily to Porcher Island. The Mahalanobis distance between Chatham Sound and Porcher Island samples was significant in 1975 but insignificant for all other years and areas.

TABLE 2. Jackknifed percentage classification success from discriminant analysis and Mahalanobis distances (D^2) between the centroids of pairs of the five geographical regions of British Columbia in 1975, 1980, and 1981. Significance of F-statistics for pairwise comparisons of D^2: $^{**}P < 0.01$.

	Queen Charlotte Islands			Prince Rupert District			Central Coast			Strait of Georgia			West coast Vancouver Island		
Geographical region	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981
Queen Charlotte Islands	75	84	77	12	7	11	9	10	21	7	2	0	2	0	0
Prince Rupert District	3 15.83**	3 7.91**	20 6.28**	80	79	75	3	10	8	0	2	0	0	2	0
Central Coast	14 4.96**	10 6.93**	0 10.15**	8 9.98**	0 8.23**	14 8.26**	79	77	71	15	4	1	0	9	11
Strait of Georgia	4 7.84**	0 15.08**	0 32.45**	0 18.86**	10 11.80**	0 35.98**	7 6.14**	3 9.02**	0 18.84**	62	73	75	6	28	29
West coast Vancouver Island	4 12.48**	3 13.24**	3 28.40**	0 36.73**	4 11.71**	0 33.47**	2 13.02**	0 7.45**	0 16.98**	16 7.57**	19 2.94**	24 1.95**	92	61	60
No. of samples	70	31	56	25	29	36	102	31	62	45	84	139	111	43	80

The plots of the canonical variates are shown in Fig. 4. The Chatham Sound samples are distinct from the other two areas in 1975, while they overlap in the subsequent two years. The few Portland Canal samples are separated from the main cluster of samples from Chatham Sound and Porcher Island in all three years. The results suggest no strong evidence for any stock separation within this region although the Portland Canal samples may represent a distinct minor stock.

Central Coast

Five separate spawning areas were identified within this region. The first four represent migratory stocks, while the few samples from several mainland inlets were combined to represent a generic minor stock. Classification success was variable, ranging between 22 and 86% (Table 3). Accuracy of classification was better than random for all areas but often only marginally so. Best results were obtained for the Mainland Inlets followed by Seaforth Channel. Misclassifications were generally concentrated within Seaforth Channel, Kildidt Sound, and Kwakshua Inlet. F-tests of the Mahalanobis distance indicate significant differences between Mainland Inlet samples and the other areas but no consistent differences among the other areas.

Canonical variates plotted in Fig. 5 show that Mainland Inlet samples differ from the other four areas in all years. Samples from the four areas representing migratory stocks generally overlap, although Kitasu Bay samples are slightly separated in 1980 and 1981. These results indicate no evidence for discrete stocks within the region except for the separation of the minor stocks within the Mainland Inlets.

Strait of Georgia and Johnstone Strait

Within this region, seven discrete spawning areas were identified for detailed comparisons. For assessment and fishery management, Deepwater Bay, Lambert Channel, Powell River, and Nanoose Bay spawning beds constitute a discrete stock as do the Gulf Islands. Classification from discriminant function analysis ranged between 19 and 100% for the seven spawning areas (Table 3). Better than random classification occurred to all areas but best results were achieved for Jervis Inlet, Deepwater Bay, and Powell River. The majority of misclassification occurred among Lambert Channel, Nanoose Bay, and the Gulf Islands. Mahalanobis distances differed significantly between Lambert Channel and all but Nanoose Bay and the Gulf Islands; Johnstone Strait differed from all but Deepwater Bay which was not different from Jervis Inlet, Powell River, and possibly Nanoose Bay.

The canonical variates in Fig. 6 suggest only that there is a clear separation of Johnstone Strait and Deepwater Bay samples from the remainder of the Strait of Georgia spawning areas. Powell River samples are somewhat intermediate, partially distinct from the other Strait of Georgia areas yet not really overlapping with Johnstone Strait samples. The few Jervis Inlet samples are clearly distinct from the other six areas within the region. The conclusions for this region are not at all clear. Johnstone Strait spawnings are distinct from those in the Strait of Georgia proper, but there is no evidence for any strong differentiation of individual spawning areas other than in Jervis Inlet. There is an indication that stocks from Deepwater Bay and Powell River may differ from the other more southerly areas, but the evidence is not conclusive.

West Coast Vancouver Island

The spawning beds for this region were subdivided into six areas representing the major sounds or inlets from south to north (Table 3). The jackknifed classification accuracy for the spawning areas in the region ranged from 40 to 93% where sample sizes exceeded two. Classification accuracy was generally much better than expected from random allocation to stocks. The greatest degree of misclassification occurred between Barkley and Clayoquot sounds and between Esperanza Inlet and Nootka and Barkley sounds.

Graphically, it is evident from canonical variate plots in Fig. 7 that samples from the southern areas (i.e. Barkley and Clayoquot sounds) are clearly different from the more northerly areas. This situation is not so pronounced in 1975, but in 1980 it is clear that the two southern areas comprise a distinct stock, as do Nootka Sound and Esperanza Inlet. The single sample from Kyuquot Sound is more similar to the latter stock. For 1981, three discrete stocks are apparent. Barkley and Clayoquot Sound samples are separate from Nootka and Quatsino Sound samples. These data suggest the existence of at least

TABLE 3. Jackknifed percentage classification accuracy from discriminant function analysis and Mahalanobis distances (D^2) for samples from geographically discrete spawning beds within each of the five geographical regions of British Columbia in 1975, 1980, and 1981. Significance of F-statistics for pairwise comparisons of D^2: **P<0.01; *P < 0.05; †insufficient degrees of freedom for valid F-statistic.

	Queen Charlotte Islands														
	Louscoone Inlet			Area 2W			Skincuttle Inlet			Cumshewa Inlet			Skidegate Inlet		
Geographical subarea	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981
Louscoone Inlet	84	50	50	0	33	7	6	29	8	13	25	7	0	0	—
Area 2W	0	10	0	100	33	72	0	0	8	0	0	0	0	0	—
	104.8**	17.8†	11.0												
Skincuttle Inlet	11	30	25	0	0	14	88	53	52	6	25	21	0	0	—
	14.6**	6.0	7.8	102.6**	23.5	9.2**									
Cumshewa Inlet	5	10	25	0	33	7	6	18	32	81	50	72	0	100	—
	12.8**	19.2	12.3	103.1**	31.6†	13.1**	15.4**	14.0	2.3						
Skidegate Inlet	0	0	—	0	0	—	0	0	—	0	0	—	100	0	—
	138.4**	54.3†		344.0†	48.6†		103.9**	41.2		115.7**	29.6†				
No. of samples	19	10	4	5	3	14	35	17	38	16	4	14	6	1	—

	Prince Rupert District								
	Chatham Sound			Porcher Island			Portland Canal		
Geographical subarea	1975	1980	1981	1975	1980	1981	1975	1980	1981
Chatham Sound	67	30	29	19	42	38	0	100	0
Porcher Island	33	50	57	62	53	62	14	0	100
	21.1**	4.2	4.6						
Portland Canal	0	20	14	19	5	0	86	0	0
	40.6	29.1†	34.3†	11.2	29.8	27.3			
No. of samples	9	10	7	16	19	29	7	1	1

	Central Coast														
	Kitasu Bay			Seaforth Channel			Kildidt Sound			Kwakshua Inlet			Mainland Inlets		
Geographical subarea	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981
Kitasu Bay	22	43	69	15	7	9	9	0	0	11	14	0	0	0	0
Seaforth Channel	22	43	22	49	57	50	45	33	22	11	14	38	0	17	25
	3.4	8.3	4.0**												
Kildidt Sound	34	0	0	32	14	18	32	34	56	17	29	12	0	17	0
	3.6	17.8†	14.8**	1.0	6.7	5.9									
Kwakshua Inlet	22	14	9	4	22	5	14	33	22	50	29	38	14	0	25
	7.1	14.4	8.3*	7.6**	9.0	5.4	5.3**	5.0†	7.9						
Mainland Inlets	0	0	0	0	0	18	0	0	0	11	14	12	86	67	50
	43.0	44.7†	13.6	39.5**	38.6**	8.2	38.9**	40.8†	12.4†	26.2**	36.2†	9.8†			
No. of samples	9	7	23	53	14	22	22	3	9	18	7	8	7	6	4

	West coast of Vancouver Island																	
	Barkley Sound			Clayoquot Sound			Nootka Sound			Esperanza Inlet			Kyuquot Sound			Quatsino Sound		
Geographical subarea	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981
Barkley Sound	50	78	74	15	7	50	10	0	0	24	0	—	0	0	—	—	—	0
Clayoquot Sound	20	22	20	68	93	42	0	0	0	10	0	—	0	0	—	—	—	0
	5.0**	8.9**	2.7															
Nootka Sound	3	0	6	5	0	8	40	67	92	14	0	—	0	0	—	—	—	11
	7.7**	29.8	16.2**	5.7**	29.1	14.0*												
Esperanza Inlet	24	0	—	12	0	—	40	33	—	45	71	—	0	100	—	—	—	—
	2.8**	49.3**		5.4**	34.9**		4.2	27.2†										
Kyuquot Sound	3	0	—	0	0	—	10	0	—	7	29	—	100	0	—	—	—	—
	13.3	46.5		23.8*	39.4		21.5†	38.2†		15.2	21.2†							
Quatsino Sound	—	—	0	—	—	0	—	—	8	—	—	—	—	—	—	—	—	89
			39.9**			32.9**			9.8									
No. of samples	30	18	46	40	14	12	10	3	13	29	7	—	2	1	—	—	—	9

TABLE 3. *(Table concluded)*

Geographical subarea	Strait of Georgia																				
	Johnstone Strait			Lambert Channel			Powell River			Nanoose Bay			Gulf Islands			Deepwater Bay			Jervis Inlet		
	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981	1975	1980	1981
Johnstone Strait	76	25	47	0	0	8	—	11	0	0	0	6	0	0	3	0	0	0	0	0	—
Lambert Channel	0	0	6	43	39	49	—	11	33	17	50	25	21	25	23	0	0	0	0	0	—
	34.8**	23.1**	8.4**																		
Powell River	—	50	22	—	0	8	—	56	67	—	25	31	—	8	3	0	0	0	—	0	—
		14.0†	5.8*		11.3**	5.1**															
Nanoose Bay	3	0	19	14	33	14	—	0	0	33	0	19	26	25	12	0	5	50	0	0	—
	36.4**	21.6†	5.3**	5.6	1.2	2.1*		8.0	4.8												
Gulf Islands	0	0	0	43	25	19	—	11	0	33	25	13	42	42	59	0	0	0	0	100	—
	26.7**	23.7	12.1**	3.5	2.5	2.0**		13.9	10.2**	4.0	4.3	3.6*									
Deepwater Bay	13	25	6	0	3	2	—	11	0	17	0	6	11	0	0	92	95	50	0	0	—
	13.6**	8.9	18.3	13.0	17.9**	18.0**		8.3	24.0†	13.0	16.2**	15.2	6.3*	19.4**	16.5						
Jervis Inlet	8	0	—	0	0	—	—	0	—	0	0	—	0	0	—	8	0	—	100	0	—
	25.9*	84.5†		43.7†	77.5**			83.7†		38.7†	79.8†		35.6	67.4†		28.8	77.5				
No. of samples	38	4	32	7	36	78	0	9	9	6	8	16	19	12	34	13	19	2	2	1	0

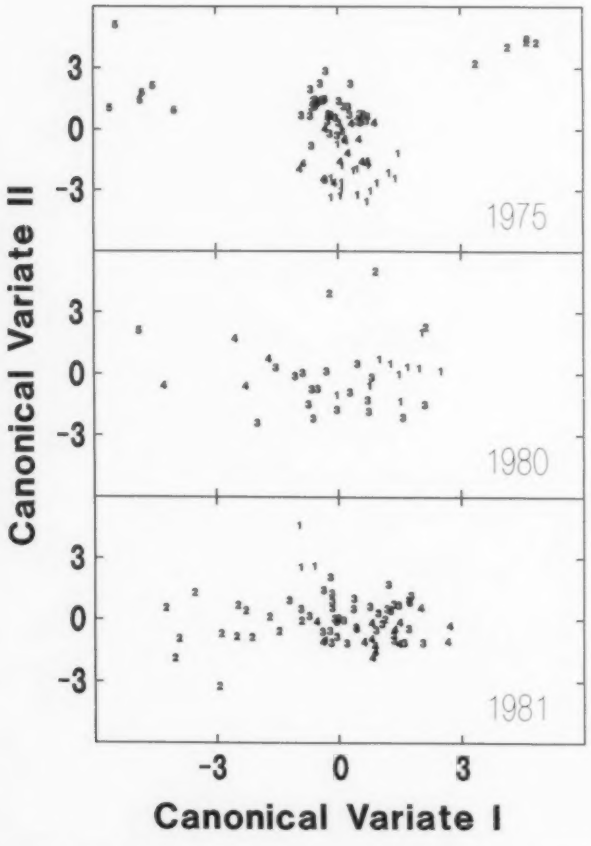


FIG. 3. Plots of the first two canonical variates for 1975, 1980, and 1981 herring samples from the Queen Charlotte Islands. See Table 1 for a description of the plotting symbols.

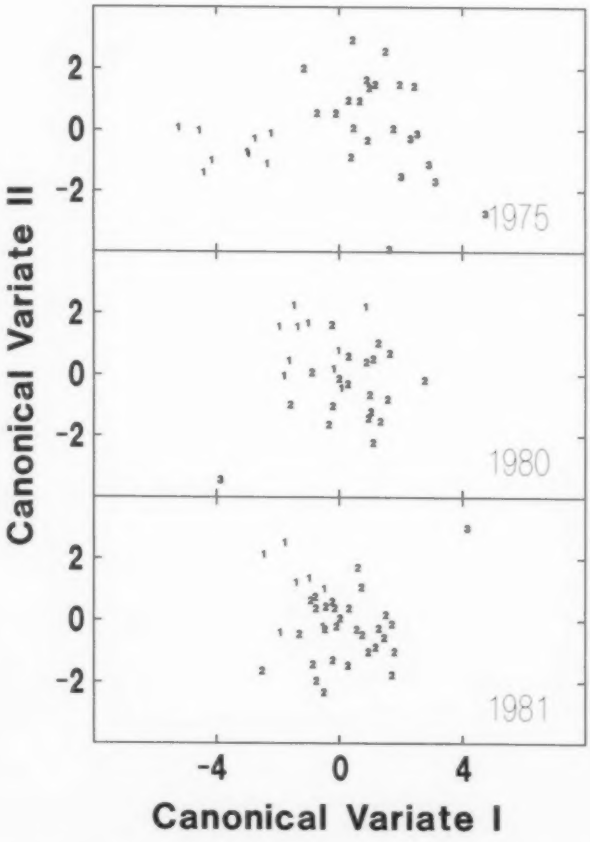


FIG. 4. Plots of the first two canonical variates for 1975, 1980, and 1981 herring samples from the Prince Rupert District. See Table 1 for a description of the plotting symbols.

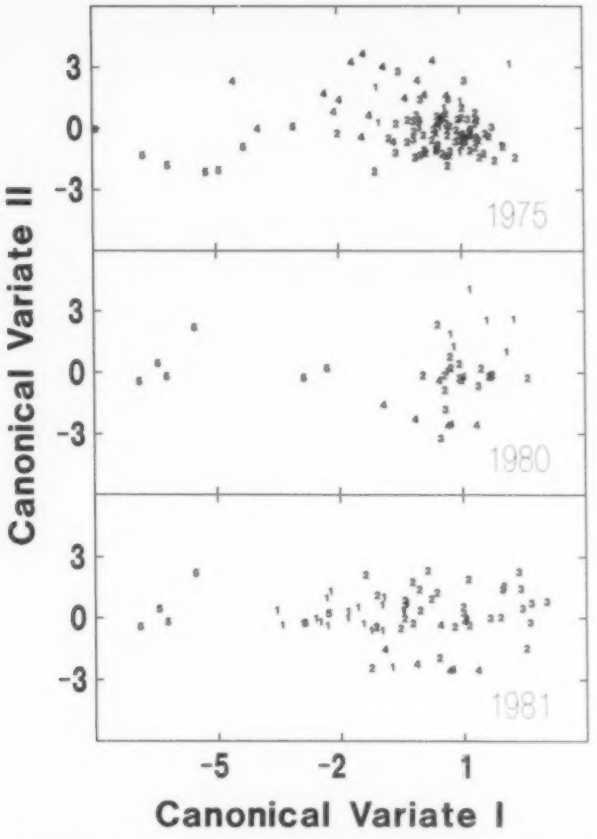


FIG. 5. Plots of the first two canonical variates for 1975, 1980, and 1981 herring samples from the Central Coast of British Columbia. See Table 1 for a description of the plotting symbols.

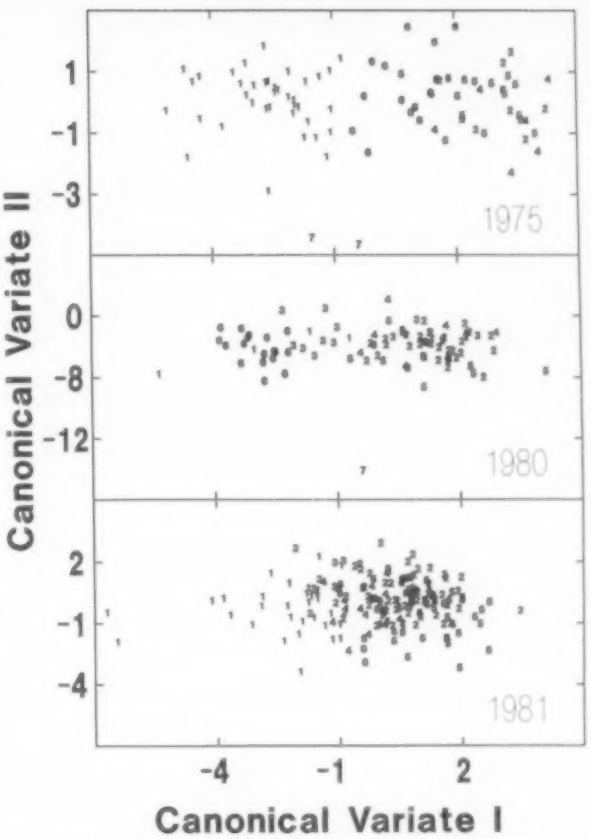


FIG. 6. Plots of the first two canonical variates for 1975, 1980, and 1981 herring samples from the Strait of Georgia and Johnstone Strait. See Table 1 for a description of the plotting symbols.

three stocks in this region. Samples from Barkley and Clayoquot sounds are clearly distinct from the more northerly areas and are somewhat differentiated from each other as well. Samples from Nootka Sound, Esperanza Inlet, and probably Kyuquot Sound form a second distinct stock. Finally, samples from the most northerly inlet in this region, Quatsino Sound, appear to be discrete from all more southerly spawning areas.

Discussion

The concept of a fish stock which is adopted for the purposes of managing a fishery is critical to the success or failure of that endeavour (Booke 1981). If the definition is too liberal, there is a great likelihood that some genetically discrete stocks will be overfished. Conversely, if the stock concept is too restrictive, it is likely that the logistics of managing the fishery will become intractable. The ideal or optimal stock concept lies somewhere in between these extremes, but in the absence of sound genetic information, fisheries managers should tend towards conservatism in an effort to separately manage as many potentially distinct spawning stocks as is practical. For the purposes of this study, a discrete stock is defined as a body of fish which occupies temporally or spatially segregated spawning beds and exhibits statistically detectable differences in the population parameters examined (Ihssen et al. 1981; MacLean and Evans 1981). Although population parameters do not provide any definitive information on genetic variability per se, they do provide recognition of stocks as separate production units. This may be important in a genetic sense and should lead to management practices which will be more conservative in terms of preserving some of the genetic integrity of the species (Ihssen et al. 1981).

The population parameters used in this study, size at age and age structure, should be reflections of differing growth and mortality rates, which could be manifestations of distinct genetic factors in different stocks. However, they could also be mediated by various environmental factors such as temperature or food production and availability. To some extent, similar arguments could be made about other variables such as morphometrics and meristics which are frequently used in stock identification studies.

As with all stock identification techniques including genetic factors such as isozymes the lack of differences in one study does not preclude the existence of stock differentiation. Conversely, true differences among samples from potential stocks indicate the possibility of genetic differences which may be subsequently verified by genetic studies. Consequently, although unusual, the variables used in this study are no less valid for stock definition than many of the more traditional

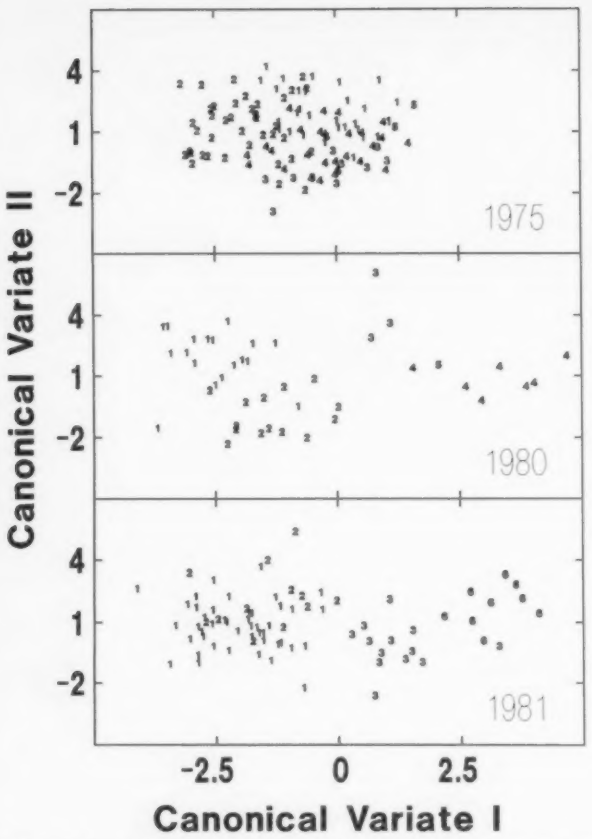


FIG. 7. Plots of the first two canonical variates for 1975, 1980, and 1981 herring samples from the West coast of Vancouver Island. See Table 1 for a description of the plotting symbols.

approaches. Any observed stock differentiation should be verified by genetic studies wherever possible.

The current stock concept for British Columbia herring identifies seven major migratory populations targeted by the roe fishery as well as a number of minor stocks (Table 1). Evidence for the existence of these various stocks comes from a number of sources. Tester (1937a) described distinct stocks in Skidegate Inlet, Chatham Sound/Porcher Island, Seaforth Channel, Deepwater Bay, Gulf Islands/Nanoose Bay, Barkley Sound/Clayoquot Sound, Nootka Sound/Kyuquot Sound, and Quatsino Sound on the basis of extensive collections of vertebral counts over several years. Tagging results essentially supported these earlier results but indicated a variable degree of intermingling among geographical regions. The available evidence indicates that 75% or more of the tagged fish returned to the same populations currently recognized, although there was also evidence of substantial homing at smaller spatial scales (Hourston 1982). Subsequent studies investigated morphometric and meristic data which indicated some differentiation on the spatial scale of an assessment region (Schweigert 1981; Meng and Stocker 1984). Recently, truss network analysis has indicated results similar to the morphometric and meristic data (Schweigert 1990). Parasite studies also support the larger scale differentiation suggested by tagging, but are unable to refine stock structure on smaller spatial scales (Arthur and Arai 1980). Finally, attempts to utilize electrophoretic and mitochondrial DNA analysis do not support any genetic differentiation of herring stocks at any scale within British Columbia (Grant and Utter 1984; Schweigert and Withler 1990). Similar spatial disaggregation of stocks has been described in Atlantic herring (*Clupea harengus harengus*) (Wheeler and Winters 1984; King et al. 1987; Grant 1984; Kornfield et al. 1982; Kornfield and Bogdanowicz 1987; King 1985; Iles and Sinclair 1982). The absence of genetic evidence for stock differentiation does not preclude the existence of such stocks, since new techniques such as nuclear DNA analysis do suggest the ability to detect genetic differentiation in Pacific herring (R. Phillips, pers. comm.).

With the exception of the tagging data, the results from applying these various stock identification techniques to herring suggest a fairly large-scale differentiation. To a significant degree this result reflects the experimental design of most of the studies whose scope was restricted to obtaining a few samples from large, discrete geographical areas. As such, they were unable to test hypotheses about stock structure at the smaller spatial scale which is suggested by the discreteness of spawning beds within current assessment regions and the high degree of homing to many of these areas (Hourston 1982). Perhaps fortuitously, the data used in this study were collected from most of the spawning areas in British Columbia.

The results from this study clearly support a stock structure at least as disaggregated as is currently used for managing the herring roe fishery. The finding of at least three distinct stocks of fish in the Queen Charlotte Islands is consistent with information from spawn timing data and supports the thesis that fish from Skidegate Inlet are a minor stock distinct from the stocks which spawn in the southeastern Queen Charlotte Islands. Similarly, the fish from the west coast of the Queen Charlotte Islands are distinct from those on the east coast. Unfortunately, little is known of the offshore distribution of herring in this region.

The stock structure identified for the Prince Rupert District is consistent with the currently accepted single stock concept. Although there is the suggestion of separation between fish from Porcher Island and Chatham Sound, the differences are neither large nor consistent. Interestingly, some fishermen feel that they are able to visually differentiate fish from these two areas. The few samples from Portland Canal indicate the existence of what appears to be a previously undocumented minor stock.

The results of this study disagree with the current stock concept for the Strait of Georgia. Stocks in Johnstone Strait are distinct from those in the Strait of Georgia. Deepwater Bay fish are similar to both Johnstone Strait and Powell River fish and are currently included in the northern Strait of Georgia stock because large reduction catches of fish expected to spawn within the strait were taken there. The other four spawning areas appear to form a single stock which represents a continuum within the Strait of Georgia showing similarities between pairs of areas and significant differences between others. Spawn timing data suggest the existence of a discrete stock in the Gulf Islands area regularly spawning in Ganges Harbour. It is quite likely that the samples included in this study would not incorporate fish from that area, so the existence of such a stock is possible. In fact, significant numbers of adult nonmigratory herring are found each year in the various tidally active passes throughout the Gulf Islands lending further support to the existence of such a discrete stock. From the present data, only the fish from Jervis Inlet seem to suggest a clearly separate stock within the Strait

of Georgia. All other herring spawning in the Strait of Georgia enter through Johnstone and Juan de Fuca straits and then apparently disperse widely.

My findings for the west coast of Vancouver Island are generally consistent with the current stock concept which recognizes a southern stock encompassing Barkley and Clayoquot sounds and a northern stock consisting of Esperanza Inlet and Nootka Sound. Evidence is also presented in support of the existence of a discrete stock in Quatsino Sound which is in agreement with Tester's (1949) analysis of vertebral counts. There is some indication that fish from Barkley and Clayoquot sounds may be discrete, but the evidence is not as convincing as for the obvious separation of the northern and southern stocks.

The major strength of the analyses presented here is that the information utilized in this study is easy to collect and is probably already available for a large number of species. For Pacific herring, there is an added advantage in that ancillary data exist from several other methods. Given the similarities in stock structure demonstrated here and the results from other techniques, it could be useful to conduct preliminary investigations of stock structure for other species where budget and manpower constraints preclude the tedious and expensive data collections and complex analyses associated with morphometric and meristic or electrophoretic studies.

In summary, multivariate analyses of a few population parameters which are routinely collected for most commercially exploited fish stocks provided statistical separation for samples of Pacific herring which was generally consistent with previous techniques of greater complexity. Yet, it indicated stock separation on a smaller spatial scale, i.e. suggesting the existence of more stocks, than had previously been indicated except by qualitative information from tagging and spawning bed distribution information (Hourston 1982; Hourston and Hamer 1979). To my knowledge, this is the first attempt to utilize this type of information in a multivariate analysis. McGlade and Smith (1983) ordinated length frequency data from samples of pollock (*Pollachins virens*) collected from different areas. Many investigators have made univariate comparisons of age composition and growth curves for samples of fish from different areas or stocks. An advantage of multivariate analysis is that it is possible to condense the information in a large number of variables while retaining much of the differentiation of the samples. The difficult question remains how to best incorporate these results into the fisheries management regime, since the accepted stock concept is usually a trade-off between biological considerations and the logistical constraints of fisheries management. Hopefully, by documenting the apparent existence of distinct stocks at a smaller spatial scale, management action will become directed towards preserving unique genetic stocks within some of these populations.

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Spawning by Hatchery-Origin Lake Trout (*Salvelinus namaycush*) in Lake Ontario: Data from Egg Collections, Substrate Analysis, and Diver Observations

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Three techniques were used to find evidence of reproductive activity by stocked lake trout (*Salvelinus namaycush*) on Stony Island reef in Lake Ontario from 1986 to 1990. In the fall, egg nets and traps were deployed on different substrate types, and in the spring, fry traps were used to capture newly emergent fry. Fry were only captured in an area approximately 50 by 10 m at the north end of the eastern edge of the reef. Eggs were only captured in nets and traps deployed near this area, or in nets and traps which moved over this area during storms and came to rest at the base of the reef. The area of Stony Island reef actually used by lake trout for egg deposition appeared to be extremely limited relative to the entire reef. This area was characterized by large cobble substrate with minimal infilling by sand and fines. Thus, hatchery-origin lake trout appeared to recognize substrate appropriate for successful egg incubation.

Trois techniques ont été utilisées pour trouver des preuves de la reproduction des stocks de truite grise (*Salvelinus namaycush*) sur le récif de l'île Stony dans le lac Ontario de 1986 à 1990. En automne, des filets et pièges à oeufs ont été déployés sur différents types de substrats, et au printemps, des pièges à frai ont été utilisés pour capturer du frai nouveau. Du frai n'a été capturé que dans une zone d'environ 50 sur 10 m à l'extrémité nord de la bordure orientale du récif. Des oeufs n'ont été capturés que dans les filets et les pièges déployés près de cette zone, ou dans les filets et les pièges qui ont traversé cette zone au cours de tempêtes pour s'arrêter à la base du récif. La zone du récif de l'île Stony réellement fréquentée par la truite grise pour y déposer ses oeufs a semblé très limitée par rapport à l'ensemble du récif. Cette zone était caractérisée par un substrat de gros galets faiblement infiltré par du sable et des corps fins. La truite grise de pisciculture a donc semblé reconnaître un substrat propice à l'incubation de ses oeufs.

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Native populations of lake trout (*Salvelinus namaycush*) disappeared from all of the Great Lakes except Lake Superior by the 1960's due to a combination of overfishing, lamprey (*Petromyzon marinus*) predation, and habitat degradation. Because of the economic and ecological importance of this species, restoration of self-perpetuating populations of lake trout has been an important goal of state, provincial, and federal fishery management agencies. Populations encompassing multiple year-classes have been established by stocking several lake trout strains as fingerlings and yearlings. However, in most lakes, evidence of successful reproduction by stocked lake trout has been limited. An understanding of the factors that limit natural reproduction would facilitate the restoration effort.

Several hypotheses for lake trout reproductive failure have been proposed, including insufficient adult stocks (Brown et al. 1981), lack of homing cues to spawning reefs (Horrall 1981; Krueger et al. 1986), inability of hatchery-raised fish to recognize appropriate spawning substrate (Krueger et al. 1986), eutrophication resulting in degradation of spawning habitats (Eshenroder et al. 1984), contaminants in the eggs (Mac 1988), egg and fry predation (Martin and Olver 1980), low fertilization rates (Ruby and Cairns 1983), and genetic incompatibilities with the environment (e.g. Brown et al. 1981). In Lake Ontario, some of these hypotheses can be rejected. Yearly assessments by the New York Department of Environmental Conservation (NYDEC) indicate that the numbers of adult lake trout at some locations in Lake Ontario exceed historic levels (Clif Schneider, NYDEC, Cape Vincent Fisheries Station, Box 292, Cape Vincent, NY 13618, pers. comm.). Eggs collected from adults in the lake each fall and raised at the Allegheny National Fish Hatchery (ANFH) had hatching rates comparable with eggs from hatchery broodstock, although extremely low hatch rates were noted in mid-1980's (David Ostergaard, ANFH, R.D. No. 1, Box 1050, Warren PA 16365, pers. comm.). No conclusive evidence has been found to suggest that contaminants in the eggs caused developmental problems. Data on fertilization rates of naturally spawned eggs are sparse and difficult to obtain, but examination of over 6700 eggs collected in the wild after natural spawning indicated that a minimum of 35–60% of the eggs were fertilized (unpublished data). Fish stocked as yearlings aggregate as adults in large numbers at traditional spawning reefs each fall, such as adjacent to Stony Island. This observation indicates that stocked lake trout can locate and use spawning reefs at least 6 km from the stocking site. However,

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several studies on reefs where lake trout aggregate in the upper three Great Lakes have failed to find evidence of egg deposition or fry emergence (Horns et al. 1989; Mark Holey, Wisconsin Department of Natural Resources, 107 N. First Place, Sturgeon Bay, WI 54235). Lake trout have also been noted aggregating at inappropriate spawning areas such as rivers in fall (Thibodeau and Kelso 1990).

A critical gap exists in our knowledge of lake trout reproduction in the Great Lakes. This gap encompasses the period between lake trout aggregation at spawning sites and the appearance of yearlings in assessment gear. In part, this information gap exists because of the logistical difficulties involved in working on the Great Lakes when lake trout are spawning and fry are emerging in late fall and early spring. Much of the published information on lake trout spawning habits and habitat comes from work in small, inland lakes, especially Canadian lakes and the Finger Lakes of New York (reviewed by Martin and Olver 1980). In contrast, no data on egg deposition or fry emergence are available from deepwater reefs in the Great Lakes, and few data are available from spawning on natural substrate (reviewed by Thibodeau and Kelso 1990). However, lake trout behavior in inland lakes may not necessarily be a good predictor of their behavior in the Great Lakes. Native lake trout were considered historically to be deepwater spawners in the Great Lakes, but in smaller inland lakes they may spawn within a metre of the surface (Royce 1951; DeRoche 1969). Stocked lake trout appear to be readily rehabilitated in inland lakes, in marked contrast with the Great Lakes.

The gap in our knowledge about lake trout reproductive behavior and success in the Great Lakes can only be filled by first finding direct evidence of spawning. Studies on egg survival, fry emergence, and reproductive success of strains are not possible without prior knowledge of the exact location of egg deposition. This paper describes research conducted on Stony Island reef in Lake Ontario to determine whether stocked lake trout deposit eggs nonrandomly with respect to substrate type. Because there has yet been no evidence of natural recruitment of lake trout in Lake Ontario, the lake trout at this site, as in the rest of the lake, are all of hatchery origin. We used a combination of existing techniques (fry traps, Stauffer 1981) and newly developed techniques (egg nets, Horns et al. 1989; egg traps, Marsden et al. 1991) to intensively examine egg deposition, the fate of spawned eggs, and fry emergence.

Methods

Study Site

All sampling of lake trout eggs and fry was conducted on a reef at the northeastern tip of Stony Island, which is located in the eastern basin of Lake Ontario (Fig. 1). This reef was a historic lake trout spawning site, and large aggregations of stocked lake trout have been noted at the reef since the early 1980's (Schneider 1985). Stony Island reef is a flat plateau which extends 180 m northeast of an exposed cobble–gravel bar at the tip of Stony Island and has a maximum depth of 5.3 m at the eastern edge of the reef. This shallow plateau is composed of gravel–pebble particles (0.8–6.4 cm) infilled with sand, with occasional large, flat rocks 20–40 cm in diameter embedded in the gravel. The total reef area, as defined by the extent of the plateau, is approximately 0.025 km^2. At its eastern edge the plateau drops steeply from 5 to 8–10 m, along a line running approximately north-northwest – south-southeast. The northwest portion of the slope is composed of large cobbles and boulders (12.8–40 cm) with interstitial spaces extending more than 45 cm below the surface of the substrate. The cobble–boulder substrate extends approximately 50 m southward from the northern end of the reef edge, and from the bottom of the slope to approximately 4 m west of the top of the slope. South of this area, the substrate along the slope is infilled with sand, and the substrate size decreases to small pebbles (1.6–3.2 cm). At the base of the reef slope the substrate is sand embedded with large cobbles. The sand is deepest at the south edge of the reef, with the embedded rocks being most exposed at the north end.

Transect Locations

Four 33 m transects were marked out on the reef on four different substrate types (Fig. 1). Transect I ran north–south along the upper edge of the northern portion of the slope, across cobble substrate. Transect II was parallel to and 10 m west of transect I and crossed gravel–pebble–sand substrate on the plateau area. Transect III ran north–south along the upper edge of the southern portion of the slope, along gravel–cobble–sand substrate. The northern end of transect III was 47 m south of the southern end of transect I. Transect IV ran north–south along predominantly sand substrate east of the bottom of the slope, in deep water (8–10 m). The distance from the bottom of the slope to transect IV varied from 3 to 15 m between years. Divers positioned the transects using compass bearings, visual observations of the substrate and the edge of the reef, and a 100 m rule on a hand spool. In 1987 and 1988 the transects were marked at either end with buoys anchored by two or three cinder blocks chained together. However, these anchors often moved during fall storms. In 1989, we used 50 kg pillow-shaped concrete anchors which were buried by divers below the surface of the substrate at either end of each transect.

Substrate Samples

To obtain quantitative measurements of the four substrate types, divers collected three substrate samples from each transect. A sample was taken at both ends of each transect and at approximately the middle. For each sample the divers removed substrate by hand from within a 42 cm diameter circular frame and placed the material into a reinforced plastic garbage bag within a 10 L plastic bucket. Substrate was removed from within the transect until the bucket was half full, so that each sample contained a uniform volume of material. Divers were careful to include embedded fines in the sample; however, loss of fines during sample collection was unavoidable, but was consistent between samples. Once the sample was complete the plastic bag was tied closed to retain fines and the bucket was marked with a buoy for later retrieval from the surface.

Each substrate sample was measured by washing the material through a series of five sieves with the following opening sizes: 2.5 cm, 1.2 cm, 3.4 mm, 2.0 mm, and 1.0 mm. The largest size class of rocks (those that did not pass through the 2.5 cm sieve) was additionally subdivided into two size classes (>10 cm and 2.5–10 cm) by measuring the largest dimension of each rock. The volume of particles in each size class was measured by placing the material in a beaker and adding a known volume of water, which was then subtracted from the total volume in the beaker.

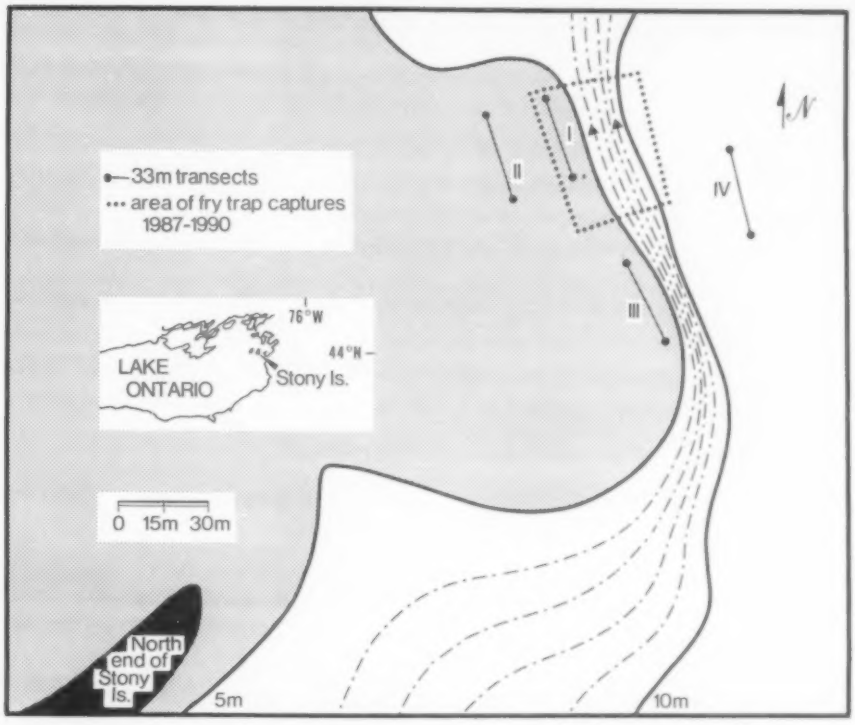

FIG. 1. Stony Island reef at the northeastern tip of Stony Island in Lake Ontario showing location of fry traps and lines of egg nets and traps described in the text. The shaded area indicates the portion of the reef above the 5 m contour.

Fry Trapping

Lake trout fry were collected on Stony Island reef in the spring from 1986 to 1990 using emergent fry traps (Stauffer 1981) modified as described by Marsden et al. (1988). Trapping was conducted between the first 2 wk in April and the first week in June. All traps were checked for the presence of fry approximately every 7 d. In 1986, 40 traps were deployed approximately 10 m apart in four lines of 10 traps each. This grid of traps encompassed most of the central part of the plateau area. The easternmost traps were located near the upper edge of the slope. On May 9 the traps were all moved adjacent to the northern and central part of the slope to maximize the concentration of traps where fry were being caught (Fig. 1; Marsden et al. 1988). In 1987, 100 traps were deployed in an area approximately 150 m from north to south and 15 m from west to east along the northern half of the top of the slope. From 1988 to 1990, 60 traps were concentrated in a smaller portion of this same area, covering approximately 100 m from north to south and 15 m from west to east (Fig. 1).

Egg Trapping

Egg nets (Horns et al. 1989) and egg traps (Marsden et al. 1991) were used to collect lake trout eggs on Stony Island reef from 1987 to 1989 (Table 1). On October 13, 1987, a line of 25 egg nets was deployed along the top of the slope overlapping the south end of transect I, and a second line of 25 nets was deployed on sandy substrate 7 m east of the bottom of the slope (transect IV). The first line of nets was retrieved and reset on transect I on November 13 and was retrieved on November 24. In 1988, lines of 25 egg nets were set along each of the four transects described above. All lines used in 1987 and 1988 to attach traps consisted of 40 m of nylon rope with nets attached every 1.6 m. The positioning of the lines was determined using the transect buoys. The lines were lifted and replaced every 3–15 d. Whenever possible the locations of the lines of nets were checked by divers after deployment and prior to retrieval. In 1989 the sampling effort was repeated as in 1988 using egg traps attached every 1.3 m to 33 m lengths of 5 mm proof coil chain.

Results

Substrate Samples

The substrate on Stony Island reef was composed primarily of limestone cobble, sand, silt, and fines. Substrate samples from transect I were unique among the samples due to the absence of any material smaller than 2.5 cm and the large volume of boulders (>10 cm; Fig. 2). Samples from transects II and III had similar volumes of all size classes of material measured. Samples from transect IV had high volumes of fines smaller than 1 mm and suspended particles, which were present in only trace amounts in the other transects. The volume of this suspended material was not measured. Two to three freshwater mussel shells (*Lampsilis radiata siliquoidea*) per sample were present only in the samples from transect IV.

Underwater photographs taken every 3 m along each transect provided a comparison of substrate sizes, but did not reveal the

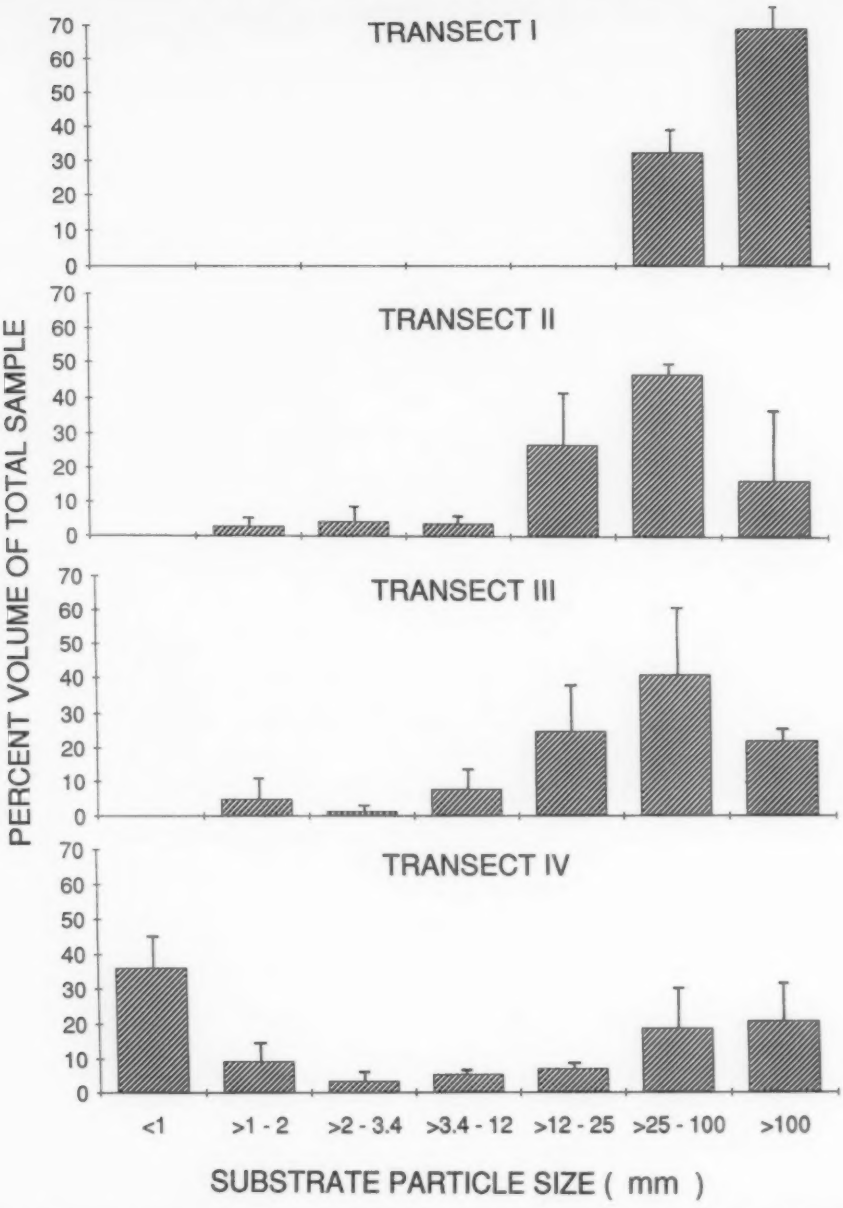

FIG. 2. Average percent volume ($N = 3$) of particle sizes from substrate samples taken on Stony Island reef, Lake Ontario, 1989. Bars indicate 1 standard error. The transect numbers refer to locations indicated in Fig. 1 and described in the text.

presence of sand or the depth of the interstitial spaces. For example, many areas along transect II appeared similar in photographs to areas in transect I, despite the presence of large quantities of sand and silt below the surface layer in transect II.

During the summer, the large cobble and boulders on the edge of the slope were covered in filamentous algal growth (*Cladophora* spp.) up to 17 cm thick. Little or no filamentous algal growth appeared on the plateau area and the southern edge of the reef, although many rocks had thin encrustations of bryzoans, freshwater sponges, and diatoms. By late October the entire upper portion of the reef was free of algal cover. However, the rocks at the north end of the reef, at the bottom of the slope, retained mats of algae. Two steel posts which were set 1 m into the upper and lower edges of the reef slope in 1988 remained in place through the spring of 1991, indicating that little or no movement of the substrate occurred at these locations. Crayfish (*Orconectes* sp.), slimy sculpins (*Cottus* sp.), darters (*Etheostoma* spp.), trout-perch (*Percopsis omiscomaycus*), and American eel (*Anguilla rostrata*) were frequently noted in the interstitial spaces among the rocks.

Small-mouth bass (*Micropterus dolomieui*) were abundant in spring and summer, and spawned along the upper edge of the reef. Other species found on and adjacent to the reef are listed in Marsden et al. (1988).

Fry Trapping

In 1986, 75 lake trout fry were captured only in fry traps deployed along the slope at the eastern edge of Stony Island reef (Marsden et al. 1988). No fry were captured in traps deployed on the plateau. The number of fry caught each day and the number of traps containing fry increased after the traps were all moved to the edge of the reef in early May 1986. Higher numbers of fry were captured in 1988–90 when all of the traps were concentrated along the northern portion of the eastern edge of the reef (Fig. 1). Fry captured in the first half of the trapping period each year were newly hatched sac fry. Extensive movement of fry at this stage of development was unexpected and suggested that fry may also have moved laterally within or across the substrate from their hatching location.

Egg Trapping

In 1987, the line of egg nets deployed along the upper edge of the slope (transect III) collected 261 eggs from October 13 to November 13. All but 29 of the eggs (11%) were collected in the nine nets set furthest to the north. All of the nets which contained seven or more eggs also contained quantities of algae, silt, and snail shells. Nets on the line which was reset on transect I collected 1830 eggs from November 13 to 24. All but 62 of the eggs (3%) were collected in 12 nets on the northern half of the transect line. The line of egg nets deployed on the sand on transect IV collected three eggs from October 13 to November 13 (Table 1). Although the position of the nets was not checked before retrieval, the quantity of debris in the nets combined with subsequent observations (see below) suggested that the nets had moved to the base of the reef after deployment.

In 1988, egg captures were difficult to correlate with the substrate on which they were collected, due to movement of the lines of nets during storms. Less than 6% ($N = 190$) of the total eggs captured in 1988 were collected in nets that remained in place between deployment and retrieval (Table 1). Most of the nets that remained in place during the trapping period were on transect IV, on sandy substrate. These nets captured 106 eggs. Because the prevailing wind direction was west to east, the nets always moved in an easterly direction. Nets which were set on transects I, II, and III, and which moved off the edge of the reef before retrieval, captured 1086, 1284, and 1134 eggs (Table 1).

In 1989, egg traps remained in place between deployment and retrieval due to the weight of the chain which held them. However, the traps were checked less often than in previous years due to storms which prohibited work on the reef. In addition, several traps were lost prior to retrieval, apparently because movement of traps during storms placed stress on the clips connecting the traps to the chain. Traps on transect I captured a total of 19 eggs; traps on transect IV captured a total of 636 eggs; no eggs were captured on transect III, and 3 were captured on transect II. One end of the line of traps set on transect IV had shifted adjacent to the base of the reef; the nine traps closest to the base of the reef collected 70 eggs whereas the 12 traps distal to the base of the reef collected 7 eggs. The line of traps retrieved from transect IV on October 22 contained unusually high quantities of algae, which suggested that underwater currents had been moving debris around.

The highest numbers of eggs were captured in 1987 in egg nets, and the lowest numbers were captured in 1989 in traps. Captures per unit effort were similar in nets in 1988 (0.270 eggs·net^{-1}·d^{-1}) and traps in 1989 (0.257 eggs·trap^{-1}·d^{-1}). The high capture rate in 1987 (1.27 eggs·net^{-1}·d^{-1}) appears to be due to the movement of the nets into a depositional zone at the base of the reef.

By the end of October in each year of the study, eggs could readily be found by divers in the vicinity of transect I by looking into the crevices between rocks. Late in November, as many as 12 eggs could be found under a single rock. Eggs were only occasionally noted near transects II (shallow plateau) and III (southern edge of the reef slope) and never on the sand beyond a metre past the base of the slope. However, large numbers of lake trout eggs were observed at the base of the reef on November 7, 1989, after a storm. Eggs observed near transect II were resting on the surface of the substrate and moved when wave-generated surge was present. In spring (April–May), divers occasionally saw dead lake trout eggs near transect I, but they never saw live eggs or fry. Dead eggs, because they are opaque white, are much easier to see than translucent live eggs.

Adult lake trout were observed on the reef during each year of the study as early as October 14 and as late as December 6. At times as many as 20 lake trout could be observed within a visibility radius of 2.5–3 m. The highest concentrations of lake trout were seen along the top of the north end of the slope. Lake trout were never seen along the south part of the slope and were only rarely seen more than 10 m west of the slope. Spawning coloration in the form of dark lateral stripes, noted by DeRoche (1969) and Royce (1951) in males, was never seen. However, this coloration may only be present at night, when spawning occurs. Pair swimming was occasionally observed, and lake trout were seen leaping at the surface. This behavior has also been noted by Merriman (1935) and Royce (1951).

Discussion

Our studies on Stony Island suggest that, even on a relatively small reef, the portion of a reef actually used by lake trout for egg deposition may be extremely limited in area. Data from egg captures, fry captures, and direct observation of adult lake trout and eggs in situ all suggested that the majority of spawning occurs only along the northern half of the eastern slope of Stony Island reef. This area is approximately 50 m from north to south and 10 m from east to west and comprises less than 5% of the total area of the reef. The substrate in this area is characterized by a high volume of large rocks (>10 cm in diameter) and an absence of sand and fines (Fig. 2). All other substrates on the reef contained high ratios of fines to larger substrate.

The egg collection data at first appear difficult to interpret due to the movement of egg nets during 1987 and 1988. However, the consistent movement of drifting nets from west to east must be taken into account. All lines of nets which captured large numbers of eggs (>80), with one exception (transect IV, retrieved November 22, 1989), passed across and over the edge of the reef and came to rest at the base of the reef (Table 1). Traps and nets which remained in place on transects I, II, and III over the period of immersion tended to capture few eggs (<30; Table 1); however, in 1987 and 1988, few lines of nets remained in place on these transects. These data suggested that

TABLE 1. Lake trout eggs captured on Stony Island reef in Lake Ontario using egg nets and traps. The number of nets or traps retrieved from each substrate type is given in parentheses. I, II, III, and IV refer to the transect locations described in the text. For example, I indicates a line of nets and traps which remained on transect I between deployment and retrieval; I–IV refers to a line of nets and traps which were deployed on transect I and drifted toward transect IV before retrieval.

Date deployed	Date retrieved	Location of egg nets and traps							Year total
		I	II	III	IV	I–IV	II–IV	III–IV	
					1987 (nets)				
Oct. 13	Nov. 13				3 (21)			261 (24)	
Nov. 13	Nov. 24					1830 (23)			
Total eggs					3	1830		261	2094
Percent					0.1	87.4		12.5	
Total trap-days					651	253		744	
					1988 (nets)				
Oct. 15	Oct. 20	12 (25)		27 (25)		0 (25)		2 (25)	
Oct. 20	Oct. 31				1 (25)	20 (25)		14 (25)	
Oct. 31	Nov. 15				5 (25)	191 (25)	774 (25)	662 (25)	
Nov. 15	Nov. 22				56 (22)	704 (22)	510 (25)	399 (25)	
Nov. 22	Nov. 25	10 (25)	6 (24)	22 (25)	6 (24)				
Nov. 25	Dec. 8		*1* (22)		38 (25)	171 (22)		57 (23)	
Total eggs		22	13	49	106	1086	1284	1134	3694
Percent		0.6	0.4	1.3	2.9	29.4	34.8	30.7	
Total trap-days		200	358	200	1201	1215	550	1249	
					1989 (traps)				
Oct. 14	Oct. 24	1 (24)							
Oct. 14	Oct. 26		1 (22)	0 (25)	0 (10)				
Oct. 24	Oct. 31	17 (18)							
Oct. 26	Oct. 31		2 (20)	0 (20)	0 (22)				
Oct. 31	Nov. 7		0 (18)		77 (18)				
Nov. 7	Nov. 22	1 (13)	0 (6)	0 (3)	559 (21)				
Nov. 22	Dec. 6	0 (22)							
Total eggs		19	3	0	636				658
Percent		2.89	0.46	0.00	96.66				
Total trap-days		869	580	445	671				
Total eggs, 1987–89		41	16	49	745	2916	1284	1395	6446
Percent of total eggs		0.6	0.3	0.8	11.6	45.2	19.9	21.6	
Eggs per trap per day		0.04	0.02	0.08	0.3	1.99	2.33	0.7	

the movement of the nets and traps is associated with the capture of eggs. Eggs may have been captured mostly at the base of the reef after travelling down the slope. Because the prevailing wind direction, and therefore surge direction, is west to east, and due to the protecting wall of the slope, the base of the reef is a zone of particle deposition. Dislodged research equipment almost invariably ended up at the base of the reef; after heavy storms, windrows of algal debris were seen in a narrow line within half a metre of the base of the slope, and on one occasion large numbers of lake trout eggs were observed at the base of the reef after a storm. Thus, eggs that were deposited at the top of the slope and were not entrapped into

the substrate may have drifted over the edge of the reef and come to rest at the base of the reef. Any nets lying at the base of the reef would collect these eggs in large quantities. This hypothesis is supported by the observation that nets containing large quantities of eggs also tended to contain large quantities (up to 10 cm^3) of sand and algae. The sand, in particular, could only have been picked up by movement of the nets and/or substrate at the base of the reef. This hypothesis would also explain why, of the nets and traps which remained in place, those deployed on the sandy substrate (transect IV) close to the base of the reef sometimes collected many eggs. These eggs would have been remnants of those drifting off the edge of the reef. Because transect IV was located at least 3 m from the base of the reef, and sometimes considerably further away, fewer eggs were collected by nets and traps on this transect than in nets and traps from transects I and II that moved to the base of the reef.

If the above explanation is valid, the majority of eggs were captured while they drifted, rather than being deposited directly by lake trout into the nets and traps. The presence of two eyed eggs in an egg net which had been deployed for only a week is conclusive evidence that drifting eggs can be captured by egg nets. Alternatively, eggs could have been spawned at the base of the reef. This hypothesis is unlikely for several reasons. Lake trout were rarely seen at the base of the reef; inasmuch as male lake trout may either lek or defend spawning territories (Foster 1985), none of them appeared to have established territories at the base of the reef. Lake trout eggs were observed by divers at the top of the slope throughout the spawning season, but were not observed on sand beyond a metre from the base of the reef. Fry were captured on the top of the reef and along the slope, indicating that at least some eggs may have been present at the top of the reef throughout the winter. However, we cannot be certain how far fry move laterally within the substrate between hatching and capture in fry traps. Eggs were unlikely to have drifted from the base of the reef to the top of the slope due to the negative buoyancy of the eggs, prevailing wind direction, and reef contours. These observations support the hypothesis that many of the eggs captured at the base of the reef were not spawned there, but drifted into the nets from the top and slope of the reef. Consequently, most of the egg capture data cannot be used to estimate the number of eggs directly deposited by lake trout per unit area because we cannot determine how many eggs drifted into the nets and traps.

Drifting of lake trout eggs has been noted repeatedly in the Great Lakes and has been hypothesized as a cause for major loss of eggs (Dorr et al. 1981). In extreme cases, windrows of eggs have been observed along beaches adjacent to spawning areas after heavy storms (Dorr et al. 1981). In their study of a natural lake trout spawning reef on the eastern shore of Lake Michigan, Dorr et al. (1981) noted that the largest concentrations of eggs occurred in shallow inshore areas which were exposed to wave action and ice scour. These eggs may have drifted eastward with prevailing wind-induced currents from deeper spawning substrate into shallow water. Clearly, the orientation of a spawning reef with respect to the shore and to prevailing winds may be an important factor for reproductive success of lake trout. Eggs deposited on a reef adjacent to a windward shore of an island may drift into unsuitable habitat. In contrast, eggs deposited on Stony Island reef, which is leeward of the island in prevailing winds, drift toward suitable substrate into which they can become entrapped. The few eggs observed on the gravel–pebble substrate in the center of the reef were not entrapped into the substrate and appeared to be vulnerable both to drifting and predation. These eggs were unlikely to have remained in the vicinity to hatch in the spring. This supposition is confirmed by the observation that none of the fry traps deployed across the plateau in 1986 captured fry. However, eggs spawned on the plateau could potentially drift eastward and become entrapped into the cobble substrate near the slope. Eggs readily drop into crevices, as noted by turning over rocks (this study; Royce 1951). Despite the presumption that lake trout eggs are highly sensitive to perturbation 48 h after fertilization (Piper et al. 1982), our observations indicated that eggs which drift for some time before becoming entrapped are often still viable. The eggs we captured in egg nets and traps, which could have been up to 2 wk old and were subjected to rough handling, had an average hatching rate of 40% when incubated in a small hatchery at Cornell University (Horns et al. 1989; unpublished data).

Capture of eggs by nets and traps was higher on the northern end of the reef than on the southern end. Of the nets that drifted, those that drifted across the north end of the slope (transect I to IV) collected an average of 1.99 $eggs \cdot net^{-1} \cdot d^{-1}$ whereas nets that drifted across the south end of the slope (transect III to IV) collected an average of 0.7 $eggs \cdot net^{-1} \cdot d^{-1}$ (Table 1). Nets deployed on the plateau (transect II) that drifted across the north end of the slope into deeper water collected 2.33 $eggs \cdot net^{-1} \cdot d^{-1}$. In 1987, nets at the north end of each line collected the majority of eggs. Based on these data, lake trout appeared to spawn preferentially on the northern end of the reef, an area characterized by large substrate and an absence of sand and fines.

What are the factors which make the northeast end of Stony Island reef an attractive place for lake trout to spawn? Several features appear to be important, including substrate size, interstitial depth, and contour. The area of maximal fry emergence, where the majority of eggs and adult fish were observed, was the area with the largest substrate particle size and the deepest interstitial spaces. The decrease in the number of fry, eggs, and adults observed from north to south along the edge appeared to be correlated with the decrease in depth of interstitial spaces and decrease in particle sizes. This result is not surprising; most of the observations of lake trout spawning have stressed the importance of large interstitial spaces for egg entrapment (Royce 1951). Substrate size is directly correlated with the size of the interstitial spaces. The fact that reproductive activity was concentrated at the upper edge of a steep slope may be simply a consequence of the reef structure, i.e. large substrate with interstitial spaces was found only at the edge of the reef. However, spawning at the edge of a steep slope may have a biological basis. First, the edge of the reef may serve to lead lake trout to the area of optimum substrate and, incidentally but importantly, to an area where other lake trout will be congregating. Thus, attraction to a steep slope could be a behavioral cue to ensure the finding of a mate in fall. Second, the physics of current flow along the edge of the reef may be important for egg incubation. The current in Lake Ontario tends to flow in a counterclockwise direction. Any current adjacent to the reef will thus flow along the edge of the reef and may tend to keep the substrate at the edge of the reef clean of silt and organic debris. Depth may also be important, i.e. stocked lake trout may not spawn deeper than 5 m. However, the absence of cobble substrate at the deeper areas of Stony Island reef prohibited testing of this hypothesis.

Several observations in inland lakes and in laboratory experiments have indicated that lake trout clean areas of spawning substrate (Royce 1951; DeRoche 1969; Foster 1985). This behavior cannot effectively prevent silt or organic material from suffocating eggs during the winter, especially in the Great Lakes where winter storms can move organic material onto reefs. Considering that all salmonids except lake trout actively use sweeping motions to build a redd for their eggs, the cleaning behavior in lake trout may be a remnant of a taxon-wide behavior. Foster (1985) suggested that this behavior is related to scent-marking the reef. We suggest that the salmonid redd cleaning behavior may be adapted in lake trout for detection of appropriate spawning substrate. Divers on Stony Island reef noted that areas of large cobble substrate infilled with sand to within 15 cm of the surface could not be distinguished by passive observation from areas of cobble with deep interstitial spaces. The presence of infilling was only apparent after lifting rocks. Lake trout may detect the presence of infilling by "cleaning" behavior. Powerful sweeping motions of the tail in areas of infilled cobble would produce clouds of silt in the water and a different current deflection than in less infilled areas. Lake trout may continue this behavior across the substrate until no silt is detected and thus find areas where spawned eggs will be entrapped successfully.

In conclusion, our data suggest that stocked, hatchery-origin lake trout which aggregate at spawning reefs deposit their eggs nonrandomly with respect to available substrate. This conclusion has two important implications for the rehabilitation of lake trout in the Great Lakes. First, despite the rearing of lake trout in raceways throughout their critical imprinting period, at least some adults are able to find spawning reefs and apparently identify substrate which will support egg incubation. However, we do not know what percentage of lake trout adults find "good" spawning substrate. Lake trout have been noted aggregating near the mouths of several rivers and travelling upstream in tributaries of Lake Ontario (Clif Schneider, NYDEC; John Fitzsimons, CCIW, pers. comm.). These fish may be seeking the currents which they experienced in the hatchery during their imprinting period. Second, the relative paucity of direct evidence of lake trout spawning in the Great Lakes may be due to the substrate specificity of egg deposition. On Stony Island reef, lake trout appear to use less than 5% of the reef area for spawning. Thus, detailed information about reef structure and substrate type may be essential for finding eggs and fry. Future studies on lake trout reproductive success would benefit greatly from data that would permit evaluation and prediction of the suitability of Great Lakes reef areas for lake trout reproduction. The present study suggests that the variables which lake trout use to select a spawning site include substrate size, interstitial spaces, a contour break, and possibly prevailing currents. This information may assist researchers in selecting sites for further investigation.

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Size Scaling of Whole-Body Maximal Enzyme Activities in Aquatic Crustaceans

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The relationships between body size and maximal activities of eight enzymes were measured in whole-body homogenates of the crustaceans *Macrobrachium rosenbergii*, *Artemia franciscana*, and *Daphnia magna*. Interspecifically and intraspecifically, enzyme activities per animal (Y) scale with protein weight (W) according to the allometric relationship $Y = aW^b$. Scaling exponents (b) varied with the enzyme examined and were usually different from 0.75. For enzymes such as citrate synthase, intraspecific and interspecific exponents were similar, but for enzymes associated with pathways other than aerobic metabolism, significant differences were found between species. For anaerobic enzymes such as lactate dehydrogenase, these differences may relate to interspecific differences in life history and ecology. For anabolic enzymes such as glucose-6-phosphate dehydrogenase and nucleoside diphosphate kinase, differences may relate to differences in growth rates between species.

Les relations entre la taille et l'activité maximale de huit enzymes ont été établies dans des homogénats d'organismes entiers des crustacés *Macrobrachium rosenbergii*, *Artemia franciscana* et *Daphnia magna*. Interspécifiquement et intraspécifiquement, l'activité des enzyme par animal Y est ramenée à l'échelle de la masse des protéines W selon la relation allométrique $Y = aW^b$. Les exposants de mise à l'échelle b varient selon l'enzyme examinée, différant en général de 0,75. Pour des enzymes telles que la citrate synthase, les exposants intraspécifique et interspécifique sont semblables, mais pour les enzymes associées à des voies autres que le métabolisme aérobie, des différences importantes ont été trouvées entre les espèces. Pour les enzymes anaérobies comme la lactate déshydrogénase, ces différences pourraient tenir à des différences interspécifiques tant génétiques qu'écologiques. Pour les enzymes anaboliques comme la glucose-6-phosphate déshydrogénase et la nucléoside diphosphate kinase, les différences pourraient tenir à des différences de taux de croissance entre les espèces.

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The phenomenon of disproportionate change in metabolic rate processes with body mass has been established in animal groups representing many phyla (Peters 1983). Such "size scaling" may be described using the allometric equation

$$(1) \quad Y = aW^b$$

where Y is the metabolic rate, W is some measure of body mass, and a and b are empirically derived constants. The constant b (here referred to as the "scaling exponent") is often found to be near 0.75 for whole-organism measures of aerobic metabolic rate (e.g. oxygen consumption) (Schmidt-Nielsen 1984).

Attention has been given to establishing precise values for the scaling exponent, explaining why the 0.75 exponent is found (see Peters 1983) and comparing inter- and intraspecific size scaling in both vertebrate and invertebrate taxa (Hemmingsen 1960; Heusner 1982; Wheatly 1989). Only in vertebrate groups, however, has research focussed on suborganismal processes.

A particularly interesting line of inquiry in suborganismal work concerns the size scaling of maximal enzyme activities. While processes such as oxygen consumption are confined to aerobic metabolism, enzymes in different pathways may be used to examine specific components of metabolism (i.e. anaerobic, anabolic, catabolic, etc.). Enzyme scaling analyses in fish and mammals have shown that the 0.75 paradigm does not always hold; lactate dehydrogenase activity scales to exponents greater than 1.0 (Somero and Childress 1980; Emmett and Hochachka 1981).

In the present study we extend examination of enzyme size scaling to one invertebrate group, the Crustacea. Crustaceans represent a useful experimental group in which respiratory scaling has been carefully examined (Weymouth et al. 1944; Hemmingsen 1960; Banse 1982; Wheatly 1989). Rapid growth rates within species allow specimens to be obtained over a large size range in short periods of time, while within the group, large variations in size may be found. From a practical viewpoint, crustaceans are economically important both as food items for human populations as well as intermediates in food webs in aquatic ecosystems (Rigler and Downing 1984). In programs of aquaculture or environmental monitoring, metabolic rates and correlates such as enzyme activity may be extremely useful. Therefore, detailed knowledge of how different types of metabolism and enzyme activity vary with body size is essential.

Invertebrates such as crustaceans present two practical problems for enzyme scaling studies. First, there is the need for an

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accurate means of assessing size which will apply across species of varying life history and morphology. Crustaceans are much more highly variable in body composition than are mammals (Corner and O'Hara 1986) and this can lead to greater variation in size scaling relationships. One common index, live or fresh weight, cannot be applied to smaller aquatic organisms, since it is often difficult to uniformly remove associated water (Rigler and Downing 1984). Dry weight cannot be directly determined if enzyme activity is to be measured in the same animal, and may be a biased estimate of the mass of metabolically active tissue, particularly in crustaceans where the exoskeleton is heavily calcified or large stores of lipid are found. Body protein content was selected for use in the present study, since it is readily measured in homogenates of whole animals and is generally a more constant fraction of organism composition (Schmidt-Nielsen 1984). The second problem concerns the use of tissue-specific enzyme activities. For smaller crustaceans, dissection of individual tissues is impractical. Furthermore, because the metabolism of individual tissues is not predictably related to that of other tissues nor to that of the whole animal in terms of respiration rate (Schmidt-Nielsen 1984), or enzyme activity (Somero and Childress 1980; Emmett and Hochachka 1981; Ewart et al. 1988), the results obtained in tissue analyses are not clearly applicable to whole-animal size. One alternative is to attempt a whole-animal enzyme measurement.

To examine the relationship between whole-animal enzyme levels and body size in invertebrates, enzymes were selected on the basis of their metabolic functions. Citrate synthase (CS) is a key regulatory enzyme in the citric acid cycle and gives a quantitative estimate of aerobic capacity (Somero and Childress 1980). Pyruvate kinase (PK) was chosen as an indicator of glycolytic capacity, while lactate dehydrogenase (LDH) served as an index of anaerobic potential. To assess amino acid metabolism the enzymes alanine aminotransferase (ala AT), aspartate aminotransferase (asp AT), and glutamate dehydrogenase (GDH) were selected. GDH may also be related to excretory processes (Bidigare and King 1981). As indices of general biosynthesis, two enzymes were chosen: nucleoside diphosphate kinase (NDPK), which provides nucleoside triphosphates for use in a variety of synthetic pathways, and glucose-6-phosphate dehydrogenase (G6Pdh), a hexose monophosphate shunt enzyme which provides NADPH for fatty acid, amino acid, and nucleic acid synthesis.

Materials and Methods

Experimental Animals

The crustaceans selected were freshwater forms with the exception of *Artemia franciscana* which was grown in half-strength seawater. Prawns (*Macrobrachium rosenbergii*) were obtained from Ontario Hydro, Toronto, Ontario, and maintained for 2 wk at 25°C prior to use. Animals were fed a commercial salmonid diet (Diet 84G, Martin Feed Mills Ltd., Elmira, Ontario) ad libitum. Brine shrimp (*Artemia franciscana* SFB, San Francisco Bay Brand, Newark, CA), hatched from cysts, were maintained in 15‰ seawater (Instant Ocean Brand, Aquarium Systems, Mentor, IL) at 25°C and fed an infusorium (Lawrence 1981). *Daphnia magna* (Northwest Biological Supply, Guelph, Ontario) were kept at 25°C following the culture techniques of Lawrence (1981) for 3 mo before sampling. At this point, individuals were reproducing parthenogenically. Freshwater copepods (*Cyclops* spp. and *Eurytemora* spp.) and ostracods (unidentified) were isolated from local ponds and maintained at 25°C.

Enzyme Extraction and Assay Procedures

Prawns were killed by decapitation, blotted dry, dissected as necessary, and weighed. Whole animals or body parts were homogenized in ice-cold 50 mM imidazole buffer (5 mL of buffer to 2 g wet weight), pH 7.2, using a Polytron PT10 unit (Kinematica GMBH, Luzern, Switzerland) for three bursts of 10 s each. Homogenates were centrifuged at 18 000 *g* for 20 min and the supernatant used directly in enzyme assays. Preliminary experiments showed that if the pellets were rehomogenized, extracted, and assayed for citrate synthase, the activity was less than 5% of that recovered in the supernatant. To verify that insoluble protein lost in the pellet did not bias body size estimates for larger animals, body wet weight was regressed against protein weight. Microcrustaceans (*Artemia*, *Daphnia*, copepods, and ostracods) were homogenized whole in 50 mM imidazole buffer (50–1000 $\mu L \cdot individual^{-1}$) using a Megason PA-300 sonicator (Ultrasonic Instruments International, Farmingdale, NY) at maximum setting for three bursts of 10 s each. For copepods and ostracods, it was necessary to pool between 10 and 25 similar-sized individuals, which were separated into size classes using 175-, 250-, and 350-μm sieves. Because preliminary centrifugation of microcrustacean homogenates produced no pellet or visible precipitate, centrifugation was not performed for subsequent measurements.

Maximum enzyme activities were determined using a Varian DMS 100 UV-Visible spectrophotometer (Varian Canada, Inc., Georgetown, Ontario) equipped with a thermostatted cell changer maintained at 25 (±0.1)°C. Reaction rate was determined by increase or decrease in absorbance of NADH or NADPH at 340 nm. Citrate synthase was monitored at 412 nm using 5,5′-dithiobis 2-nitrobenzoic acid (DTNB). Enzyme activity was expressed as units per animal where one unit equals 1 μmol of substrate converted to product per minute. Conditions for assay procedures were adapted from Hochachka et al. (1970) and Emmett and Hochachka (1981) with substrate and cofactor concentrations optimized to give maximum activity. All assays for cytoplasmic enzymes were conducted in 50 mM imidazole, pH 7.2, while the mitochondrial enzyme citrate synthase was assayed at pH 8.2. Such pH values approximate in situ pH for the respective enzymes (Roos and Boron 1981). Other conditions were as follows:

Citrate synthase (CS), EC 4.1.3.7: 0.1 mM DTNB, 7.0 mM $MgCl_2$, 0.3 mM acetyl coenzyme A, 0.5 mM oxaloacetate (omitted for control).

Lactate dehydrogenase (LDH), EC 1.1.1.27: 0.2 mM NADH, 100 mM KCl, 2.0 mM sodium pyruvate (omitted for control).

Pyruvate kinase (PK), EC 2.7.1.40: 0.2 mM NADH, 5.0 mM ADP, 50 mM KCl, 10 mM $MgCl_2$, 5.0 mM phosphoenolpyruvate (omitted for control), and excess LDH.

Alanine aminotransferase (ala AT), EC 2.6.1.2: 200 mM L-alanine, 0.2 mM NADH, 0.025 mM pyridoxal phosphate, excess LDH, and 10.5 mM alpha-ketoglutarate (omitted for control).

Aspartate aminotransferase (asp AT), EC 2.6.1.1.: 0.2 mM NADH, 7.0 mM alpha-ketoglutarate, 0.025 mM pyridoxal phosphate, excess malate dehydrogenase, and 30 mM L-aspartate (omitted for control).

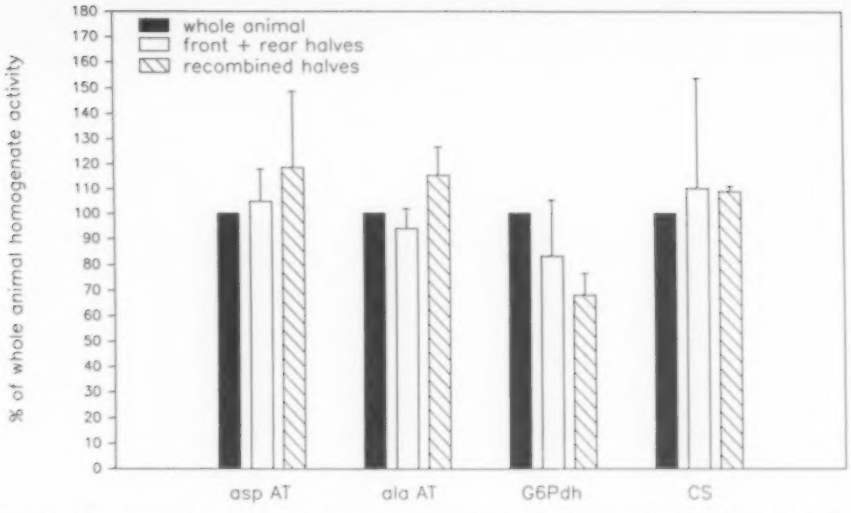

FIG. 1. Relative activities of aspartate aminotransferase (asp AT), alanine aminotransferase (ala AT), glucose-6-phosphate dehydrogenase (G6Pdh), and citrate synthase (CS) in *Macrobrachium rosenbergii* using different homogenization procedures. Activities are expressed as percentages of the activity of the whole-animal homogenates. Values are means ± SE for four determinations.

Glutamate dehydrogenase (GDH), EC 1.4.1.2: 0.2 mM NADH, 250 mM ammonium acetate, 0.1 mM Na_2EDTA, 1.0 mM ADP, and 14.0 mM alpha-ketoglutarate (omitted for control).

Nucleoside diphosphate kinase (NDPK), EC 2.7.4.6: 0.2 mM NADH, 20 mM $MgCl_2$, 2.0 mM ATP, 70 mM KCl, 1.1 mM phosphoenolpyruvate, excess LDH, excess PK, and 0.7 mM thymidine diphosphate. Two controls were run, one omitting homogenate and the other omitting thymidine diphosphate (Agarwal et al. 1978).

Glucose-6-phosphate dehydrogenase (G6Pdh), EC 1.1.1.49: 0.4 mM NADP, 7.0 mM $MgCl_2$, 1.0 mM glucose-6-phosphate (omitted for control).

Protein assays were performed on homogenates with a microassay procedure using coomassie brilliant blue dye (Bio-Rad Laboratories (Canada) Inc., Mississauga, Ontario) with bovine serum albumin as the standard. Preliminary experiments showed that imidazole buffer did not affect linearity of the assay.

Validation of Whole-Body Enzyme Measurements

The use of whole-animal versus single-tissue homogenates was conveniently validated in *Macrobrachium rosenbergii*. The posterior body segment of *Macrobrachium* is composed predominantly of the abdominal flexor muscle (virtually a single tissue), while most of the intestine and the hepatopancreas are localized in the anterior segments. Pairs of animals, closely matched in size, were selected over as large a range of body size as possible. One animal in each pair was homogenized whole, while the second was separated into two parts at the posterior margin of the carapace and each part homogenized separately. For a representative subset of enzymes, asp AT, ala AT, G6Pdh, and CS, four different assays were performed in duplicate. Whole-animal homogenate was used in the first assay. The second and third assays were performed on anterior body homogenate and posterior body homogenate individually. To differentiate homogenization artifacts (for example, decreased whole-animal activity due to increased time to homogenize) from unfavorable interactions of homogenate components, anterior and posterior body homogenates were mixed in proportions relative to anterior/posterior wet weights and assayed. Activities were statistically compared within each enzyme in a one-way ANOVA, with $P < 0.05$ considered to represent a significant difference.

Scaling Experiments

Duplicate or triplicate assays for CS, LDH, PK, ala AT, asp AT, GDH, NDPK, and G6Pdh were performed on animals over as wide a size range as possible within *Macrobrachium* ($n = 18$ or $n = 22$), *Artemia* ($n = 46$), and *Daphnia* ($n = 20$). Copepods ($n = 6$) and ostracods ($n = 2$) were included for comparison only and were not used in subsequent regression analyses due to the small sample size.

Protein weights and enzyme activities per whole animal were log-transformed (common logarithm) to linearize the allometric equation (Peters 1983). Activity of each enzyme was regressed against protein weight for each species and for all species combined using SAS General Linear Models procedure (SAS Institute Inc., Cary, NC). Tests of the null hypotheses $b = 1.0$, indicating direct proportionality of enzyme activity with body weight, and $b = 0.75$ (the scaling exponent often found for metabolism–weight relationships) were performed in all cases. Tests of homogeneity of slope ($b_{Daphnia} = b_{Macrobrachium} = b_{Artemia}$) were performed and differences were investigated using paired Student t-test comparisons for unequal variance (Steel and Torrie 1980). For all statistical comparisons, $P < 0.05$ was considered to represent a significant difference.

Results

Validation of Whole-Body Enzyme Measurements

Mean activity of homogenates (Fig. 1) demonstrate the similarity of results for each homogenization procedure. In the

TABLE 1. Summary of regression analyses, fitting the model $\log Y = \log a + b \log W$.[a]

Enzyme	Species	Model parameters[b]				P values for H_0[d]	
		$\log a$	b	r^2	%SEE[c]	$b = 0.75$	$b = 1.00$
CS	*Daphnia*	−3.58 ± 0.34	0.814 ± 0.188	0.69	327.0	0.74	0.36
	Macrobrachium	−4.06 ± 0.98	0.892 ± 0.175	0.69	80.4	0.44	0.55
	Artemia	−3.97 ± 0.11	0.975 ± 0.064	0.88	35.4	0.01	0.70
	All species	−3.86 ± 0.08	0.865 ± 0.025	0.96	120.0	0.01	0.01
LDH	*Daphnia*	−3.55 ± 0.33	0.916 ± 0.179	0.76	76.0	0.39	0.66
	Macrobrachium	−4.12 ± 0.27	1.120 ± 0.050	0.98	48.3	0.01	0.03
	Artemia	−3.34 ± 0.12	0.984 ± 0.071	0.87	40.1	0.01	0.82
	All species	−3.61 ± 0.08	1.050 ± 0.020	0.98	102.1	0.01	0.03
PK	*Daphnia*	−2.66 ± 0.26	0.227 ± 0.141	0.16	55.8	0.01	0.01
	Macrobrachium	−3.39 ± 0.23	1.080 ± 0.040	0.98	40.6	0.01	0.08
	Artemia	−2.86 ± 0.18	0.696 ± 0.106	0.59	64.9	0.62	0.01
	All species	−3.61 ± 0.06	1.120 ± 0.020	0.98	76.4	0.01	0.01
ala AT	*Daphnia*	−2.77 ± 0.10	0.540 ± 0.063	0.85	36.5	0.01	0.01
	Macrobrachium	−3.68 ± 0.16	1.010 ± 0.030	0.99	27.4	0.01	0.80
	Artemia	−3.87 ± 0.13	1.150 ± 0.080	0.88	45.0	0.01	0.07
	All species	−3.52 ± 0.03	0.973 ± 0.011	0.99	51.4	0.01	0.01
asp AT	*Daphnia*	−3.21 ± 0.14	0.835 ± 0.078	0.93	27.7	0.31	0.07
	Macrobrachium	−3.60 ± 0.17	1.010 ± 0.030	0.99	28.7	0.01	0.67
	Artemia	−2.93 ± 0.13	0.710 ± 0.077	0.74	44.0	0.60	0.01
	All species	−3.35 ± 0.03	0.967 ± 0.011	0.99	42.4	0.01	0.01
GDH	*Daphnia*	−3.19 ± 0.20	0.652 ± 0.111	0.81	41.8	0.41	0.02
	Macrobrachium	−4.73 ± 0.34	0.949 ± 0.060	0.96	64.9	0.01	0.42
	Artemia	−4.44 ± 0.17	1.020 ± 0.100	0.79	59.4	0.01	0.84
	All species	−4.15 ± 0.05	0.848 ± 0.015	0.98	61.1	0.01	0.01
NDPK	*Daphnia*	−1.91 ± 0.09	0.194 ± 0.054	0.49	30.8	0.01	0.01
	Macrobrachium	−2.18 ± 0.10	0.888 ± 0.018	0.99	16.1	0.01	0.01
	Artemia	−2.33 ± 0.08	0.857 ± 0.049	0.91	25.2	0.04	0.01
	All species	−2.50 ± 0.04	0.919 ± 0.017	0.97	96.7	0.01	0.01
G6Pdh	*Daphnia*	—	—	—	—	—	—
	Macrobrachium	−4.42 ± 0.21	0.907 ± 0.037	0.98	36.2	0.01	0.03
	Artemia	−4.53 ± 0.18	1.070 ± 0.100	0.78	63.9	0.01	0.54
	All species	−4.25 ± 0.05	0.883 ± 0.017	0.98	69.0	0.01	0.01

[a]Y is enzyme activity (μmol substrate converted·min^{-1}·animal^{-1}); W is protein weight (μg).
[b]Fitted parameters a and b are presented ± SE.
[c]Percent standard error of the estimate.
[d]Results of tests of the null hypotheses (H_0), $b = 0.75$ and $b = 1.00$, are given as P values.

whole-animal homogenates which are set to 100% in Fig. 1, actual mean activities (± SE) were as follows: asp AT, 0.302 (±0.031) units·mg protein^{-1}; ala AT, 0.220 (±0.026) units·mg protein^{-1}, G6Pdh, 0.021 (±0.003) units·mg protein^{-1}; and CS, 0.029 (±0.007) units·mg protein^{-1}. No significant differences were found between homogenization procedures within enzymes (asp AT, $P < 0.73$; ala AT, $P < 0.70$; G6Pdh, $P < 0.56$; CS, $P < 0.49$).

Scaling Experiments

The relationship between wet weight and protein weight in *Macrobrachium* was linear ($r^2 = 0.92$, $n = 24$). Protein comprised an average 17% of wet weight.

For all enzymes examined, regression statistics are provided in Table 1.

Regressions of CS activity versus body weight (Fig. 2) show similar results intra and interspecifically. The scaling exponent for the interspecific relationship is 0.865 which is statistically different from both 0.75 and 1.0. In intraspecific relationships, scaling exponents fall numerically between 0.75 and 1.00; however, no intraspecific exponent is statistically different from 1.0, and only for *Artemia* is the exponent greater than 0.75. No significant differences were detected between intraspecific scaling exponents ($P > 0.53$).

For interspecific regressions of both LDH and PK activity versus body weight (Fig. 3 and 4), scaling to exponents greater than 1.0 is found (1.05 and 1.12, respectively). For intraspecific regressions of LDH activity, only *Macrobrachium* shows an exponent greater than 1.0. *Artemia* and *Daphnia* have scaling exponents not significantly different from 1.0, and lower than *Macrobrachium* ($P < 0.03$, $P < 0.02$), but not significantly different from each other ($P < 0.51$). All intraspecific PK activity scaling exponents are significantly different from each other ($P < 0.01$ in all cases). The exponent for *Daphnia* is lower than 0.75, the exponent for *Artemia* is not different from 0.75, and the exponent for *Macrobrachium* is not different from 1.0.

Ala AT and asp AT activities (Fig. 5 and 6) show patterns of scaling similar to each other. Interspecific scaling exponents are numerically close, 0.973 for ala AT and 0.967 for asp AT, both significantly less than 1.0 and greater than 0.75. For

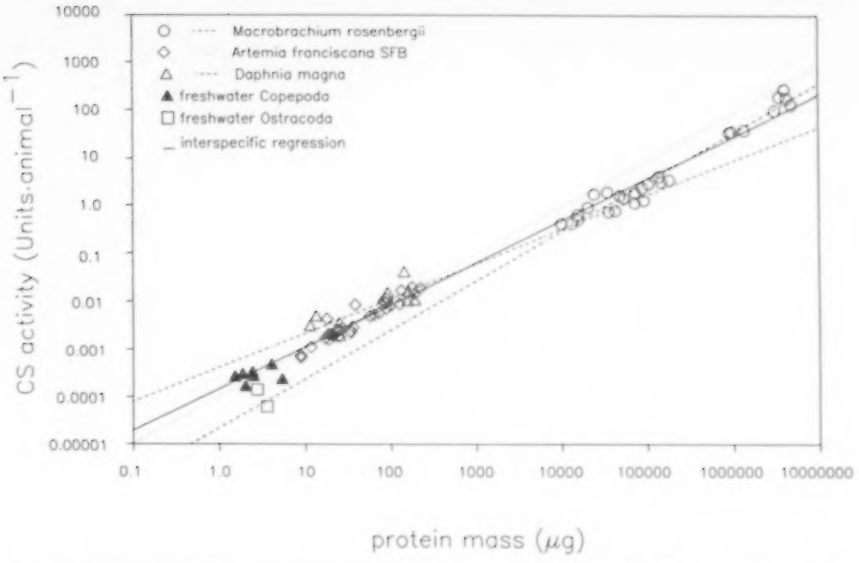

FIG. 2. Whole-animal citrate synthase (CS) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

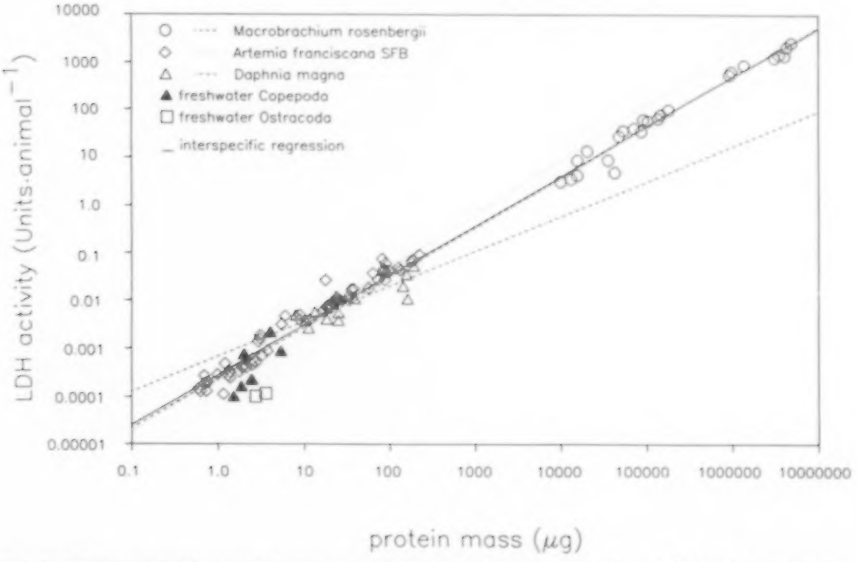

FIG. 3. Whole-animal lactate dehydrogenase (LDH) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

ala AT activity the scaling exponent for *Daphnia* lies between 0.75 and 1.0 and is distinct from the other two species ($P < 0.01$ in both cases). *Macrobrachium* and *Artemia* have scaling exponents not different from 1.0 and not significantly different from each other ($P > 0.09$). For asp AT, both *Daphnia* and *Macrobrachium* activities scale to exponents significantly different from 1.0, and not different from each other ($P > 0.12$). The scaling exponent for *Artemia*, which is not significantly different from 0.75, is lower than that of *Macrobrachium* ($P < 0.01$) but not different from *Daphnia* ($P < 0.22$).

GDH activity gives an interspecific scaling exponent of 0.848 (Fig. 7), significantly different from both 0.75 and 1.0. While *Macrobrachium* and *Artemia* showed exponents not significantly different from 1.0, *Daphnia* appeared no different from 0.75. However, no statistical differences are detectable between intraspecific scaling exponents ($P < 0.09$).

The interspecific exponent for NDPK, 0.919, is between 0.75 and 1.0 (Fig. 8). Intranspecific scaling exponents follow the interspecific trend, and are not statistically different from each other ($P < 0.35$). The exponent for *Daphnia* is significantly lower than 0.75 and distinct from *Artemia* and *Macrobrachium* ($P < 0.01$ in both cases).

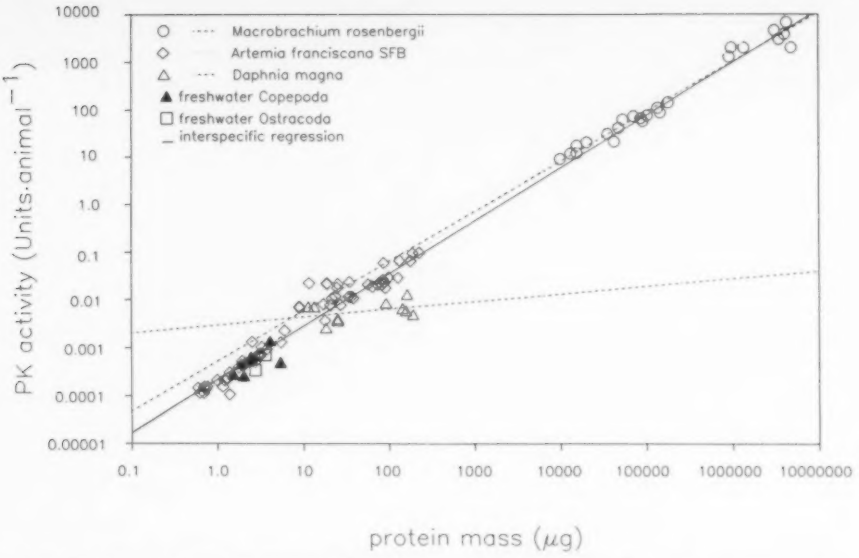

FIG. 4. Whole-animal pyruvate kinase (PK) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

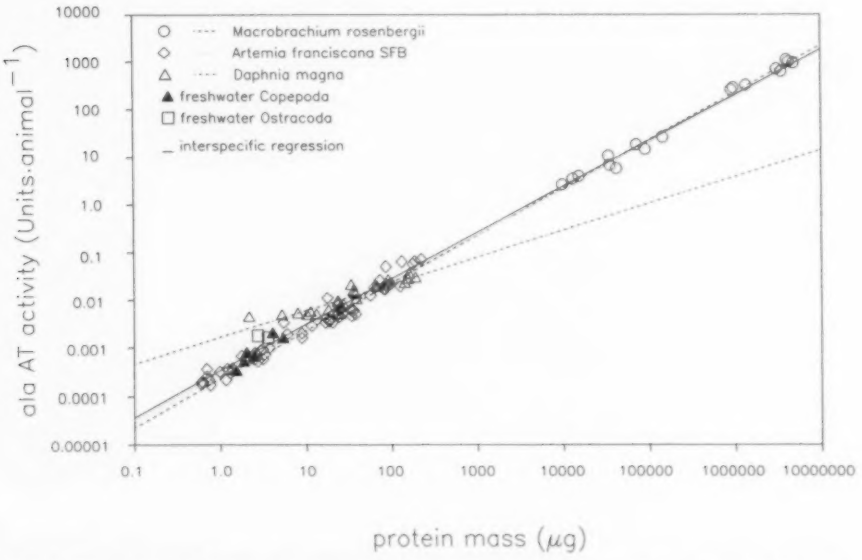

FIG. 5. Whole-animal alanine aminotransferase (ala AT) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

G6Pdh (Fig. 9) could not be reliably detected in *Daphnia* due to very low activity and the small amounts of homogenate available for assay. Interspecifically, G6Pdh activity scales to the exponent 0.883, significantly higher than 0.75 and lower than 1.0. Scaling exponents for *Artemia* and *Macrobrachium* were not significantly different from each other ($P < 0.09$), although the exponent for *Macrobrachium* was different from 0.75 and 1.00, and *Artemia* was not different from 1.0.

Based on graphical relationships, enzyme activities of copepod and ostracod species appear close to values which would be predicted on the basis of their size by interspecific scaling relationships (Fig. 2–9).

Discussion

Whole-Animal Homogenization

For the enzymes tested, whole-animal homogenization appears to provide a reasonable index of total enzyme activity. This is true for enzymes with different substrate and cofactor requirements (i.e. coenzyme A for CS, pyridoxal phosphate for ala AT and asp AT, and NADPH for G6Pdh, as well as those in different cellular compartments (mitochondrial for CS versus cytoplasmic for other enzymes).

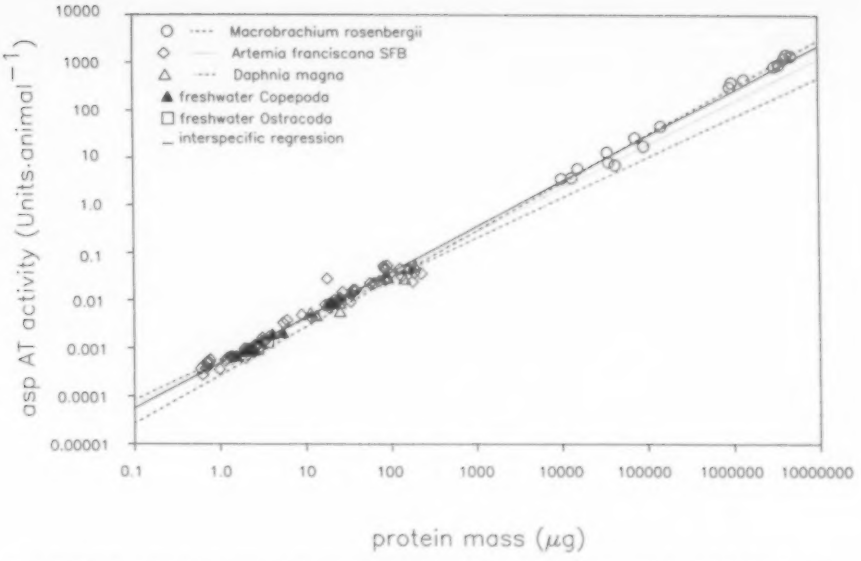

FIG. 6. Whole-animal aspartate aminotransferase (asp AT) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

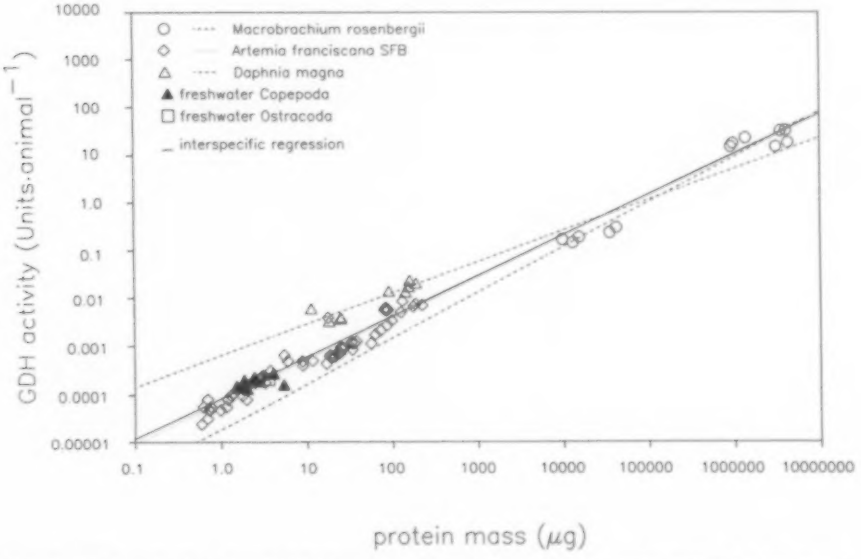

FIG. 7. Whole-animal glutamate dehydrogenase (GDH) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

Enzyme–Scaling Relationships

It has been argued that relationships between metabolic rate and body size should not be compared within and between animal groups, since interspecific scaling may involve differences in developmental stages (Hemmingsen 1960; Heusner 1982). Since the case for enzyme activity has not yet been considered in this context, and mindful of this potential problem, we have chosen to examine and compare both inter- and intraspecific scaling relationships in this study. Intraspecific comparisons are most relevant, but general trends may be most clearly demonstrated with interspecific comparisons.

Citrate synthase

CS activity is representative of maximal aerobic capacity and has been found to account for 90% of total respiration (Hochachka et al. 1970). As such, it might be expected that CS activity would scale with body size to the same exponent as that found for oxygen consumption. While mammalian interspecific data clearly indicate an exponent near 0.75 for oxygen consumption, wide variation and generally higher exponents have been reported for crustaceans. Zeuthen (1953) cited scaling exponents of 0.76 for a freshwater crayfish, 0.881 for *Daphnia*, and 1.0 for *Artemia*. Alternatively, Gilchrist (1959) found 0.883 for *Artemia*. Interspecifically, Weymouth et al.

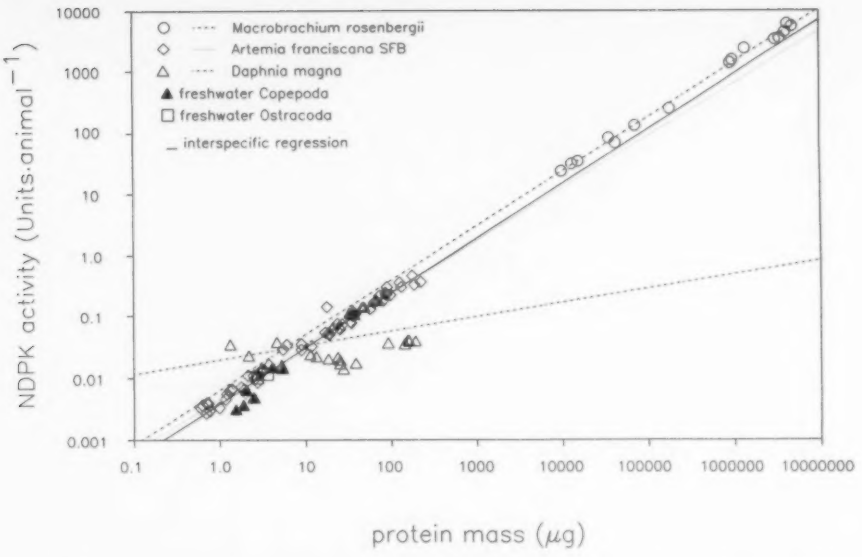

FIG. 8. Whole-animal nucleoside diphosphate kinase (NDPK) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

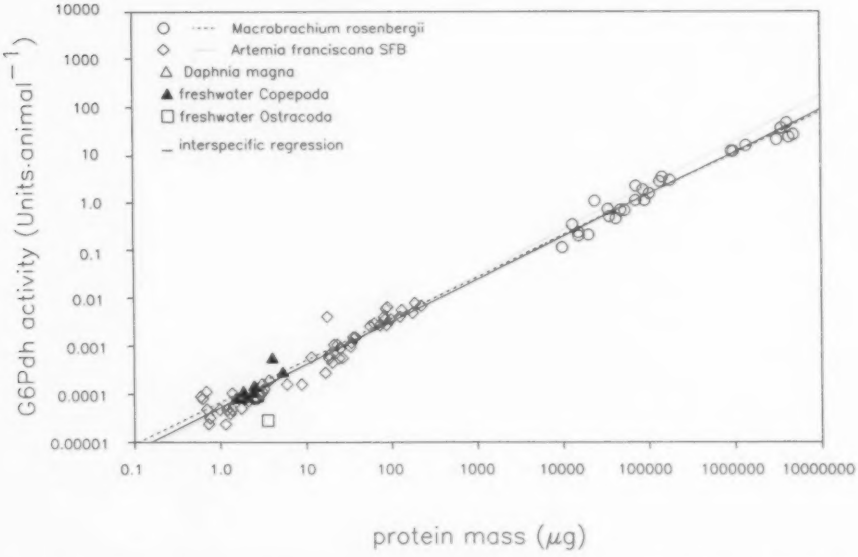

FIG. 9. Whole-animal glucose-6-phosphate dehydrogenase (G6Pdh) activity versus protein weight for five crustacean species. Regression statistics are given in Table 1.

(1944) found an exponent of 0.75 for several species of crab, and Vidal and Whitledge (1982) and Blazka et al. (1982) have shown slopes between 0.88 and 1.15 for marine and freshwater planktonic crustaceans. More recently, Wheatly (1989) calculated an exponent of 0.88 using several decapod crustacean species. These findings are compatible with scaling relationships for CS activity determined in the present study.

Scaling relationships for CS activity in fish and mammal tissues indicate an exponent of 0.75, closely matching the exponent for mammalian oxygen consumption (Somero and Childress 1980; Emmett and Hochachka 1981). Houlihan et al. (1985) reported a wet-weight-specific exponent corresponding to 0.84 in the extensor muscle of the crab *Carcinus*, close to the interspecific value of 0.87 obtained in the present study.

The similarity of intraspecific scaling exponents may indicate a fundamental similarity in the response of aerobic metabolism to changing body size.

Lactate dehydrogenase

Scaling relationships for LDH activity in fish and mammal species have been shown to vary with the tissue examined. For example, Somero and Childress (1980) noted a lack of size scaling for LDH in the brain of certain fish species, while LDH activity in muscle scaled to an exponent greater than 1.0. LDH has different functions in different tissues: it may act primarily in the lactate-to-pyruvate direction in gluconeogenic tissues or in the opposite direction in tissues engaged in anaerobic glycolysis, or in both forward and reverse directions at different times in the same tissue. In a whole-animal measurement, LDH may be more closely related to the relative proportions of different tissues, or the mode of activity of the organism. Thus, interspecific comparisons of LDH activity may be less meaningful. The fact that *Daphnia* and *Artemia* show little size scaling of LDH activity may relate to their small size; energetic requirements of small planktonic organisms relying on diffusion may not require increases in anaerobic capacity over their size ranges. Alternatively, for *Macrobrachium*, a benthic organism which relies on burst swimming responses to escape predators, size variation of LDH and hence anaerobic capacity may be greater. Somero and Childress (1980) argued that anaerobic energetic requirements for burst swimming increase as size increases. This is reflected in the exponent greater than 1.0 observed for *Macrobrachium* in the present study.

Pyruvate kinase

The role of PK in metabolism is not uniquely aerobic because oxidation of glucose via PK may proceed under anaerobic conditions. As in the case of LDH, there is tissue-specific variation; Somero and Childress (1980) reported that PK activity scales with a slope greater than 1.0 in fish muscle, but is virtually constant over size in the brain. Emmett and Hochachka (1981) and Houlihan et al. (1985) also found a positive scaling (slope greater than 1.0) in mammalian and crustacean muscle, although Ewart et al. (1988) demonstrated a slope of 0.81 for sea raven (*Hemitripterus americanus*) heart muscle. Following arguments developed for LDH, if smaller species are predominantly aerobic, PK activity might scale in a similar manner to CS, as is seen for *Artemia*. For larger crustaceans such as *Macrobrachium*, relying increasingly on anaerobic metabolism as body size increases, scaling exponents closer to 1.0 would be expected for PK, since PK does function both in anaerobic as well as aerobic glycolysis. The differences in intraspecific exponents may also be due to variation in molt status, since PK is known to vary in activity across stages of the molt cycle (Lesicki 1977). Interspecific trends are less easily compared in these conditions.

Alanine and aspartate aminotransferases

Intraspecifically, there is little pattern to variations of ala AT or asp AT scaling exponents. For the interspecific comparison, exponents are close to 1.0. Since neither enzyme can be considered to have a regulatory role in metabolism, it is difficult to predict a scaling relationship based on scaling of a particular metabolic process. Thus, an exponent near 1.0 might be what is expected for an enzyme capable of functioning either catabolically or anabolically. Presumably, in high-food environments where all sizes of animals are receiving adequate food, differences in enzyme activity across animal size based on variations in pathways of degradation or synthesis of amino acids would not be expected. Since alanine is involved in the osmoregulatory response in crustaceans (Hochachka and Somero 1984), differences in patterns of activity of ala AT between freshwater and saltwater species might have been anticipated; however, this is not apparent in the present study.

Glutamate dehydrogenase

In crustaceans where the major excretory product is ammonia, GDH activity has been suggested as an indicator of ammonia excretion (Bidigare and King 1981). Nitrogen excretion is generally found to scale to the exponent 0.75 in mammals, as does oxygen consumption (Peters 1983); thus, similar exponents for CS and GDH might be expected. In fact, Banse (1982) has argued that nitrogen excretion must scale with the same exponent as oxygen consumption; otherwise, organisms of different sizes feeding on food of similar composition would differ much more in body oxygen to nitrogen ratios than is observed in the Crustacea. Interspecifically, the present study does indeed show similar scaling exponents for both CS and GDH. Given the wide confidence intervals for intraspecific CS exponents, intraspecific CS and GDH exponents may also be comparable. Interspecific ammonia excretion exponents from Vidal and Whitledge (1982) and Blazka et al. (1982) for marine and freshwater plankton are also in this range.

Nucleoside diphosphate kinase and glucose-6-phosphate dehydrogenase

Both NDPK and G6Pdh are associated with anabolic pathways. The interspecific trend in both cases indicates exponents less than 1.0. Because anabolic processes control the amount of material available for growth, it is useful to consider the growth patterns of individual organisms with respect to differences in scaling relationships of anabolic enzymes. An exponent of less than 1.0 means that weight-specific enzyme activity decreases with increasing body size. This is compatible with the observation that larger species tend to have lower specific growth rates (Banse 1982; Peters 1983). Because growth of organisms in this study was not monitored, it is impossible to attribute differences in scaling relationships to this variable. As well, tissue-specific scaling of protein synthesis in fish indicates exponents less than 1.0, and similar to those of aerobic metabolism (Houlihan et al. 1986). Interestingly, however, in the case of both enzymes, *Daphnia* does not fit the interspecific relationships: G6Pdh could not be detected and the NDPK activity is practically invariant with body protein weight. In terms of growth and development, *Daphnia* is distinct in that it has a direct development instead of a series of larval stages. Scaling studies have paid very little attention to enzymes in anabolic pathways.

More generally, in scaling studies, differences in growth rates between animals are often ignored. Bertalanffy (1957) has suggested that anabolism should follow the surface rule (0.67 exponent), while catabolism will be directly proportional to body weight (1.0 exponent). If this is true, then animal metabolism might be expected to display scaling values near 0.67 during rapid growth when anabolism predominates and nearer 1.0 during senescence when catabolic processes are more important. Evidence from Schmidt-Nielsen (1984) shows that mammalian growth rate itself scales with body mass during postnatal linear growth phases to an exponent between 0.67 and 0.75. In another context, Goolish and Adelman (1987) have suggested that different individual tissue growth rates may confound attempts to establish relationships between tissue enzyme

activity and body size. This may apply to whole-animal studies as well. Thus, future studies of scaling relationships should take growth rate into account.

In summary, from the present study, the following conclusions may be drawn. First, whole-animal homogenization is a valid method for estimating whole-animal enzyme activity, in the crustaceans examined. Such measurements can provide a means of investigating scaling by dividing metabolism into its component anabolic and catabolic processes while overcoming the problems of extrapolating from single-tissue measurements. Second, size scaling of enzyme activity has been demonstrated in crustaceans for a variety of enzymes. This implies that use of enzymes to assess metabolic rates, or responses to environmental change, must take account of body size effects. Third, while intraspecific scaling is similar among species for enzymes such as CS, for others such as PK it is quite different. In cases of high intraspecific variability, the meaning of interspecific exponents must be carefully interpreted.

Acknowledgements

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Seasonal Development of Ice Algae Near Chesterfield Inlet, N.W.T., Canada[1]

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Welch, H. E., M. A. Bergmann, T. D. Siferd, and P. S. Amarualik. 1991. Seasonal development of ice algae near Chesterfield Inlet, N.W.T., Canada. Can. J. Fish. Aquat. Sci. 48: 2395–2402.

Ice algal chlorophyll *a*, (Chl), an estimator of biomass, was measured throughout the growing season (March–May) near Chesterfield Inlet on the northwest coast of Hudson Bay (63°30′N). The $\log_{10}$ transformation of Chl per square metre was a negative linear function of snow depth at any given date and location. Maximum biomass reached about 170 mg Chl·m^{-2} over deep water but only one tenth as much over shallow water. This smaller standing crop was correlated with lower concentrations of nitrate in shallow water, postulated to result from nitrogen uptake by kelp. Ice-associated amphipods were abundant but had little detectable effect on the development of ice algal biomass. Ice algal Chl over deep water was predicted closely by the model developed for Resolute at 75°N, relating Chl to overlying snow depth and cumulative surface light. It appears that, where nutrients are adequate, ice algal biomass below first-year sea ice can be predicted for much of the Arctic from two variables, cumulative surface light and snow depth.

La chlorophylle *a* (Chl) des algues de la glace, un estimateur de la biomasse, a été contrôlée pendant toute la saison de croissance (mars à mai) près de l'inlet Chesterfield sur la côte nord-ouest de la baie d'Hudson (63°30′N). La transformation $\log_{10}$ de Chl par mètre carré est une fonction linéaire négative de l'épaisseur de neige quel que soit la date ou l'endroit. La biomasse maximale atteignait environ 170 mg Chl·m^{-2} par eau profonde, mais à peine le dixième de cette valeur par eau peu profonde. Une corrélation a été établie entre ce faible peuplement et les faibles concentrations de nitrate en eau peu profonde, ce qui laisse présumer une accumulation d'azote par le varech. Les amphipodes associés à la glace étaient abondants, mais ont eu peu d'effet notable sur la croissance de la biomasse algacée de la glace. La Chl algacée de la glace par eau profonde a été prévue avec justesse par le modèle de la Chl en fonction de l'épaisseur de neige sus-jacente et de l'ensoleillement superficiel cumulé, mis au point pour Resolute à 75°N. Il semble que, là où les éléments nutritifs sont idoïnes, la biomasse algacée sous la glacede mer d'un an peut être prévue pour une grande partie de l'Arctique à partie de deux variables, l'ensoleillement superficiel cumulé et l'épaisseur de neige.

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Microalgae inhabiting the underside of first-year congelation sea ice, hereafter simply called ice algae, comprise a significant portion of total annual primary production in arctic seas (Alexander 1974; Welch and Kalff 1975; Smith et al. 1988). Ice algae in the eastern Canadian Arctic are primarily diatoms (Hsiao 1980; this study; unpubl.) and they support a complex meiofaunal community (Grainger and Hsiao 1990). They are eaten by ice-associated invertebrates, especially Amphipoda (Carey and Boudrias 1987; Lewis 1987), and provide a source of food for planktonic grazers such as *Pseudocalanus* spp. in April, May, and June before the development of the annual open-water phytoplankton bloom (Conover et al. 1986; Runge and Ingram 1988).

Despite the presumed importance of ice algal production to the trophic dynamics of the arctic marine ecosystem, the factors controlling ice algal growth and distribution are still poorly known. Four factors (light, nutrients, substrate, and grazing) can be expected to influence the growth of ice algae. Light is an important variable because ice algae grow beneath sea ice overlain by wind-drifted, relatively opaque snow, and recent work has indeed shown that available light largely controls ice algal growth during its exponential growth phase (Gosselin et al. 1985, 1986; Horner 1985; Smith et al. 1988; Welch and Bergmann 1989). Nutrients are also probably important because of supply problems from the water column to a dense, stationary algal layer growing in a matrix of ice crystals. Nutrient limitation has been demonstrated in the estuary of the Great Whale River, southeastern Hudson Bay, where maximum algal growth is correlated with high current flow caused by spring tides (Gosselin et al. 1985). But if the water column is not strongly stratified the evidence for tidal control of ice algal growth is weaker (Cota et al. 1987). Substrate can also affect ice algal biomass during melt or over brackish water, but we assume that the space available for colonization on the underside of the ice surface is not limiting when normal sea ice is actively growing (Welch and Bermann 1989). Losses to grazers also occur but there is little documentation. In Barrow Strait (≈75°N), circumstantial evidence suggests that herbivorous amphipods reduce the biomass of ice algae over shallow water (Pike and Welch 1990; Welch and Bergmann 1989) but do not affect algal growth over deep water (>75 m). The abundance of ice-associated macroinvertebrate grazers is inversely proportional to underlying water depth, becoming less than 1·m^{-2} over water depths in excess of 75 m (Pike and Welch 1990). For a comprehensive review of ice algal dynamics and physi-

[1]Contribution No. 14 from the Resolute Marine Laboratory.

ology, see Cota et al. (1991) and Cota and Smith (1991a, 1991b).

Recent work in the Canadian high Arctic, near Resolute at 75°N, has shown that ice algal biomass peaks in late May beneath low snow, at 250–325 mg chlorophyll *a* (Chl)·m^{-2} (Welch and Bergmann 1989; Smith et al. 1988). On any given date the distribution of ice algae is a log function of overlying snow depth, and this log function is applicable over may kilometres, demonstrating that ice algal growth is synchronous over very large areas (thousands of square kilometres) (Welch and Bergmann 1989). The snow–algae functions can be combined with either cumulative surface light or cumulative day of year beginning with the first day the sun reappears into a simple model which predicts ice algal biomass for any date and snow cover. Nutrient data do not increase the model precision (Welch and Bergmann 1989).

The purpose of the present work was to extend the Resolute observations to the shallow, lower latitude waters of Hudson Bay to determine if ice algal growth there could be predicted by the same snow thickness and cumulative light model and if nutrients or grazers influenced the expected relationship. We also performed photosynthesis/irradiance experiments on ice algae and combined these with data for light transmission and snow depth to calculate various photosynthetic parameters and total ice algal photosynthesis (Bergmann et al. 1991). The research was carried out near Saqvaqjuac, a Department of Fisheries and Oceans Research Station located on an inlet of Hudson Bay about 35 km north of the hamlet of Chesterfield Inlet (Fig. 1). Our plan was to monitor ice algal growth and associated parameters at a single site (station 1) and sample other locations to determine their similarity to station 1. However, partway through the study we discovered great differences in algal biomass between stations 1 and 2, necessitating monitoring of station 2 as thoroughly as our limited resources allowed.

Methods

Field Procedures

The main study sites were station 1, a relatively shallow nearshore basin of maximum depth ≥49 m surrounded by shallow sills (Fig. 1), and station 2 on the north side of the Chesterfield Inlet trough, ranging from shore to >100 m depth. Secondary sites included station 3 (100 m deep) in Daly Bay 55 km to the northeast of Saqvaqjuac and stations 4 and 5 (Fig. 1).

A series of 32 ice algal samples (often one or more was lost) was taken weekly beneath a range of snow depths at station 1 and four times beneath a range of snow depths at station 2 to define the relationship between snow depth and algal biomass. From 26 February to 16 April 1988 we used a standard 7.3-cm inside diameter SIPRE corer to sample ice algae, cutting off the bottom-most 4 cm of the ice core and taking a 5.24-cm-diameter subcore from that. After 16 April we used a subice suction corer (Welch et al. 1988) to remove a 6.0-cm-diameter by 3.0-cm-deep sample from the underice surface. Snow depth and ice thickness were measured at each core site. Details of equipment, procedures, and the calculation of algal Chl abundance are given in Welch et al. (1988) and Welch and Bergmann (1989). The estimation of mean Chl below a given snow cover was calculated from snow depth frequency distributions and Chl – snow depth functions as per Welch and Bergmann (1989).

We also made weekly observations of Chl and ice-associated amphipods along a depth transect perpendicular to shore at station 2. We first drilled a 10-cm-diameter hole and then lowered a Benthos minicamera with flash on an arm and took six pictures of the underice surface spaced equidistant around a circle 1.5 m from the hole. An ice algal sample was then taken in the center of each of three photographed areas. Snow and ice thickness measurements were made at the six spots. Amphipods were not disturbed by the auger or camera and were subsequently enumerated from the pictures (T. D. Siferd et al., in prep.).

Snow depth frequency distributions were determined on areas of sea ice judged to have uniform mean snow cover (procedures as in Welch and Bergmann 1989). In addition, a permanent 700-m snow course marked by wires stuck in the snow at 1-m intervals was laid out at station 1 and snow depths at each metre interval measured six times from 6 March to 13 May 1988.

The water column at stations 1 and 2 was sampled periodically for Si, NO_3-N, PO_4-P, and CTD profiles.

Surface light (PAR, quanta) was recorded continuously at the Saqvaqjuac Field Station with a Licor model 192S flat plate sensor mounted on the roof. The attenuation of surface light through the snow and ice and passing through the algal layer was measured using a Licor 192S sensor held in a toothed holder mounted on a remote arm deployed through the ice (Welch and Bergmann 1989). The procedure and data are discussed in Bergmann et al. (1991).

Laboratory Procedures

We used the quantity of Chl extracted from the ice algal community as our measure of ice algal abundance (Bunt and Lee 1970). Core samples were kept dark and cold until arriving at the laboratory, where they were melted and filtered through Whatman GF/C filters before passive extraction in 95% methanol and reading in a Turner model III fluorometer calibrated against lettuce Chl. Details of this procedure and the calculation of Chl per square metre are given in Welch et al. (1988). Reactive silica, NO_3-N, and soluble reactive phosphorus were analyzed according to Stainton et al. (1977) using a Technicon autoanalyzer and specifications (1977 version). Ammonia was not measured.

Results

Study Area

All work took place in 1988 on first-year shore-fast ice extending seaward to the shore lead. The shore lead at this location is a zone of open water and broken ice separating the central Hudson Bay ice sheet from shore-fast ice and is an extension of the Roes Welcome Sound polynya to the north (Fig. 1). The local sea bottom is Precambrian granitic gneiss with basins partially filled with coarse glacial sediment, gravel, and rock. There is considerable submerged local relief, similar to that presented by the adjacent rocky hills, with numerous reefs, islands, and basins in a shallow, uncharted sea. Water depths landward of the shore lead average less than 20 m, although Chesterfield Inlet itself is a relatively deep (≈100 m) east–west trench (Fig. 1). Large kelps are visibly abundant on the rocky shoals and seaward at the flaw lead.

All the small rivers in the vicinity of Saqvaqjuac freeze and no longer run by late winter, so there were no horizontal gradients in salinity due to freshwater inputs. The water in the

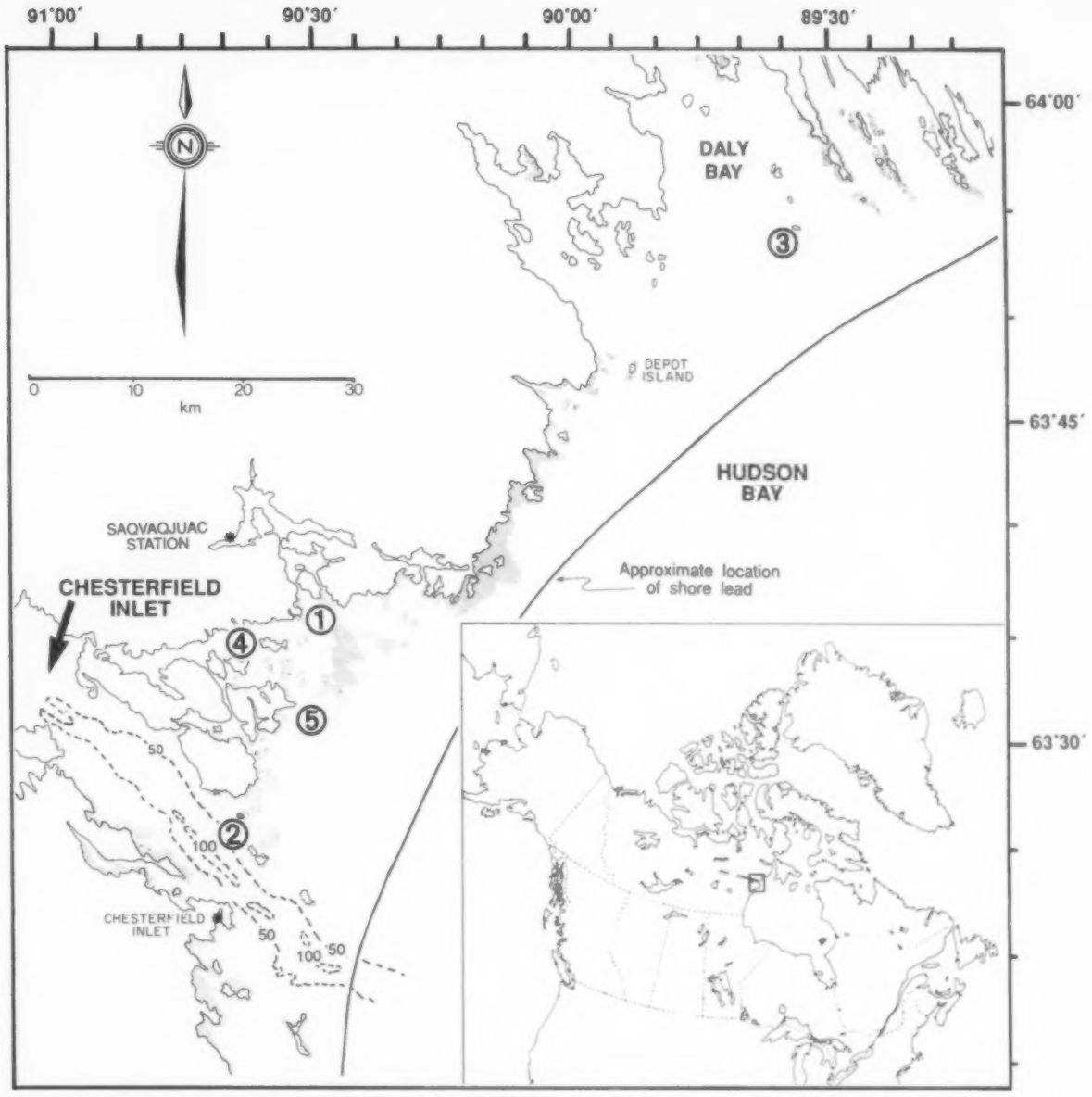

FIG. 1. Research area on the northwest coast of Hudson Bay showing sampling stations 1–5. Depth contours in metres. Nearshore bottom morphometry north of Chesterfield Inlet is unknown.

station 1 basin (Fig. 1) experienced slow tidal exchange, but a series of shallow sills separated that basin from deeper offshore water whereas station 2 water in Chesterfield Inlet circulated freely with the main body of Hudson Bay (Fig. 1). Hudson Bay is strongly stratified in summer (Prinsenberg 1988), but fall storms, wind-driven cooling in the shore lead, and cryoconcentration of brine from sea ice result in uniform temperatures and salinities top to bottom in any given location by midwinter in the Saqvaqjuac area (authors, unpubl.). The circulating water column combined with continued cooling at the shore lead, and perhaps in local polynyas such as the race between Saqvaqjuac Inlet and the sea (Fig. 1), results in frazil-ice formation, which we have observed in the water column in late winter. In ice holes, we also found several ice crystal aggregates with captured sediment which had apparently floated up from the bottom and may have contributed frazil-ice to the underside of the congelation sea ice. Although common in Antarctic waters, frazil-ice is not considered an important source of ice accumulation in the central Arctic (Maykut 1985). In nearshore western arctic seas, episodic frazil deposition results in layers of sediment being incorporated into the ice, which decreases light penetration (Maykut 1985). Several times we detected thin layers of sediment in the ice at shallow sites,

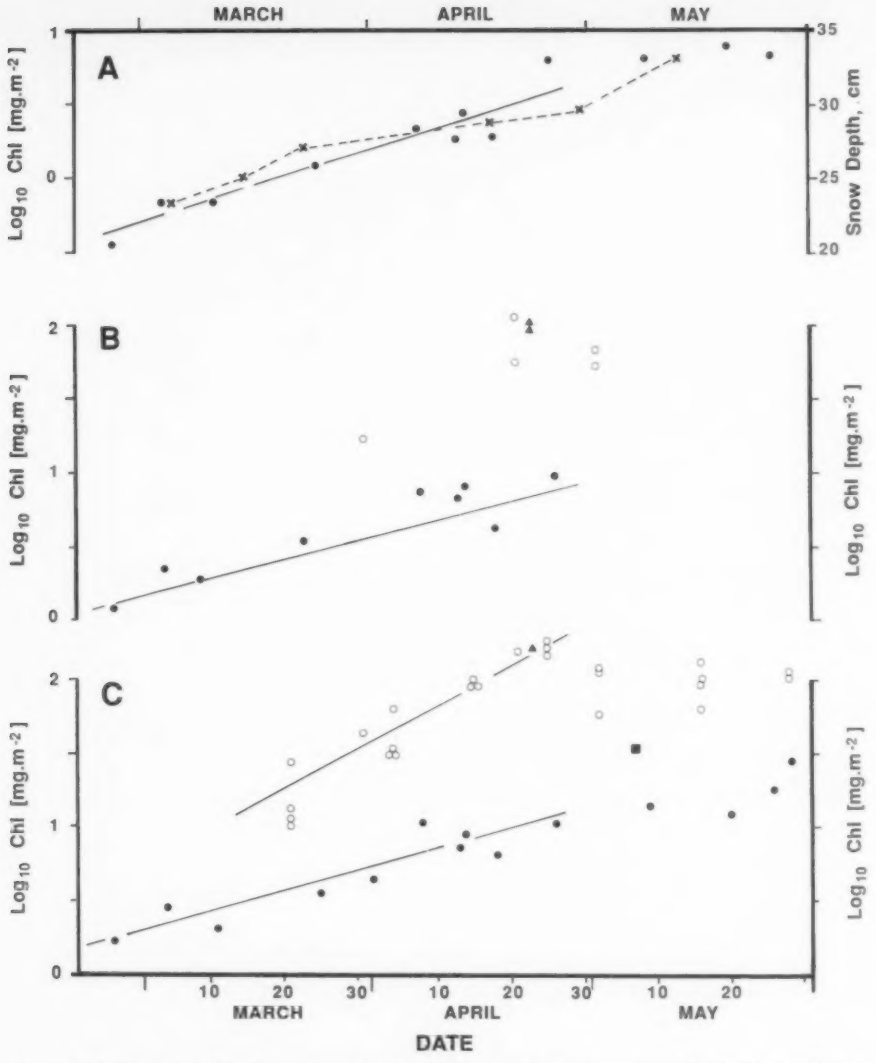

FIG. 2. (A) Mean snow depth and mean ice algal Chl at station 1. × = snow depth (N = 700 per date, from snow course), ● = Chl (N = 30–32 per date). Solid line is the regression of mean Chl against day of year from 27 February (day 57) through 28 April (day 117) where $\log_{10}$ Chl (mg·m^{-2}) = 0.0162 (snow depth (cm)) − 1.2987 (r^2 = 0.84, N = 9). (B) Mean ice algal Chl calculated for a mean snow depth of 10.1 cm from the Chl – snow depth regressions in Table 1 and the snow depth frequency data from Welch and Bergmann (1989). ● = station 1; ○ = station 2; ▲ = station 3. (C) Maximum Chl near Chesterfield Inlet in 1988. ● = station 1 where $\log_{10}$ Chl = −0.548 + 0.014 (day of year) (r^2 = 0.87, N = 10, 21.9-d doubling time, 26 February to 26 April); ○ = station 2, all sites with <10 amphipods·m^{-2} of ice surface, mean of three Chl samples per site. Regression is $\log_{10}$ Chl = −1.341 + 0.031 (day of year) (r^2 = 0.91, N = 16, 9.7-d doubling time, 21 March to 25 April); ▲ = station 3; ■ = station 4.

but the faintly visible bands did not appear dense enough to significantly alter the subice light climate.

Ice thickness at stations 1 and 2 averaged 1.2 m in late February and reached ≈1.65 m in May. Ice thickness was inversely proportional to snow depth, with the maximum range in thickness for any day and location being about 0.3 m. Snow depth increased steadily at station 1, from a mean of 20 cm in late March to 33 cm by late May (Fig. 2A), whereas snow depths were lower at station 2, with large areas having little or no snow until late May. Once drifts were established they tended to sinter in place and were not eroded by subsequent storms, although settling occurred when air temperatures approached 0°C (data from snow course, not shown). Therefore, ice algae near Chesterfield Inlet may experience reductions in light flux as a result of snow drift accumulation, but not usually increases in light due to drift erosion.

Si, NO_3-N, and PO_4-P concentrations did not vary with depth at any given site and time, indicating vertical mixing at each

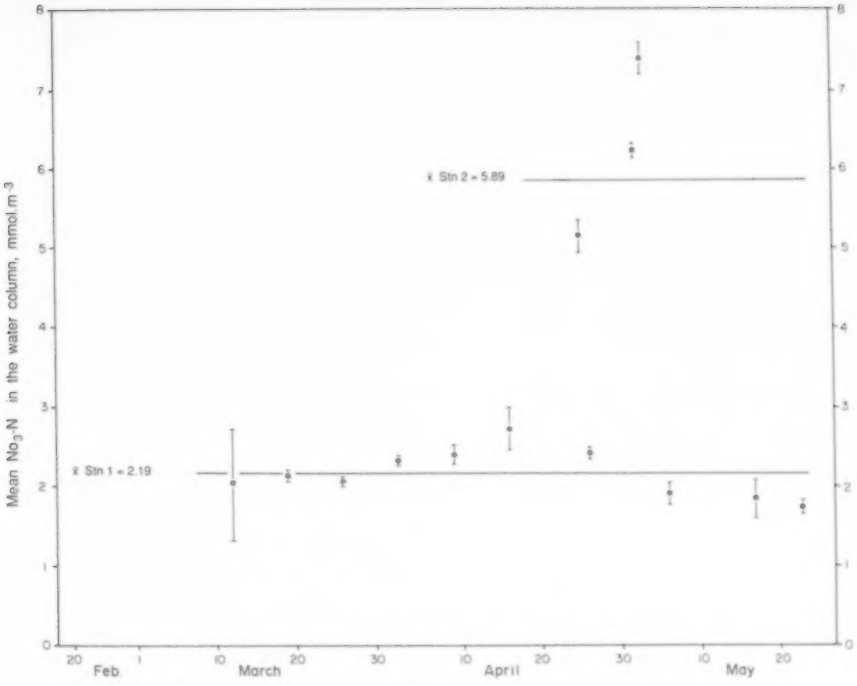

FIG. 3. Mean (±1 SD) water column NO_3-N concentrations at stations 1 and 2.

station. Si concentrations at all stations and depths were virtually constant at 10–11 mmol·m^{-3}, with slightly higher values (to 13 mmol·m^{-3}) inside Saqvaqjuac Inlet near the research laboratory. P was also quite constant at 1.2–2.0 mmol·m^{-3} over all depths and stations. However, nitrate (NO_3-N) concentrations were consistently different from site to site, being lower at station 1 and higher at station 2 on the three dates sampled (Fig. 3). Nitrate concentrations were also low in all basins inside Saqvaqjuac Inlet and at station 4, with values comparable with station 1. A single set of samples taken on 13 May at station 5 was intermediate, 4.6 mmol·m^{-3} ± 0.44 SD.

Ice Algal Development Beneath a Range of Snow Depths

As expected, ice algal Chl was highly correlated with snow depth, with $\log_{10}$ Chl at any given locality and time being a negative linear function of snow depth (Fig. 4). Regressions of $\log_{10}$ Chl against snow depth are summarized in Table 1. Slopes and intercepts were generally higher at stations 2 and 3 than at station 1 on equivalent dates because there was a higher biomass of ice algae over the deeper basins of stations 2 and 3. There was also a steady decrease in the slopes of the log Chl – snow depth relationships with time for station 1, for which there were the most data (Fig. 5). This indicates that algal growth rates beneath low snow cover gradually decreased relative to growth rates beneath higher snow cover, as the growing season progressed.

Given a distribution of snow depth frequencies and a Chl – snow depth regression, the mean Chl for a specific location and date could be calculated. Thus the application of the weekly Chl – snow depth equations (Table 1) to the six snow frequency distributions for station (not shown) gave a mean Chl less than 1 mg·m^{-2} in late February and a peak of only 8 mg·m^{-2} by May (Fig. 2A).

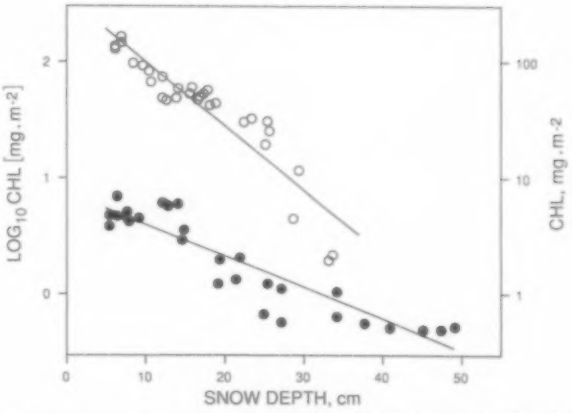

FIG. 4. Examples of the log Chl – snow depth relationships found at Saqvaqjuac during the season of exponential ice algal growth. ● = station 1, $\log_{10}$ Chl = 0.894 − 0.0275 (snow depth) (r^2 = 0.84); ○ = station 2, $\log_{10}$ Chl = 2.566 − 0.0551 (snow depth); (r^2 = 0.86).

Because we had only two sets of snow distribution frequencies for the vicinity of station 2, and because the mean snow cover varied across Chesterfield Inlet, we could not calculate the mean Chl development for the Inlet. However, given the much higher Chl at a given snow depth, and the lower snow cover near station 2 ($\bar{x}$ = 12.5 cm, N = 554, 31 March; $\bar{x}$ = 15.5 cm, n = 347, 21 April), average algal Chl must have been an order of magnitude higher at station 2 than at station 1. Ice algal Chl beneath variable snow cover at multiple sites can best be compared by applying the same snow depth fre-

TABLE 1. Coefficients for regressions of ice algal Chl on snow depth, where $\log_{10}$ Chl ($mg \cdot m^{-2}$) = a + (b) (snow depth (cm)).

Date	Station	N	a	b	r^2
26 February	1	31	0.461	−0.0444	0.71
4 March	1	32	0.710	−0.0425	0.89
11 March	1	30	0.572	−0.0314	0.60
23 March	1	31	0.794	−0.0273	0.79
31 March	2	32	1.577	−0.0389	0.47
8 April	1	32	1.167	−0.0316	0.85
13 April	1	32	1.100	−0.0305	0.62
14 April	1	32	1.291	−0.0308	0.70
18 April	1	30	0.894	−0.0275	0.84
21 April	2 (shallow water)	30	2.093	−0.0383	0.85
21 April	2 (deep water)	30	2.566	−0.0551	0.86
23 April	3 (shallow water)	34	2.326	−0.0358	0.73
23 April	3 (deep water)	35	2.383	−0.0474	0.74
26 April	1	30	1.091	−0.0099	0.75
2 May	2 (shallow water)	29	1.983	−0.0288	0.63
3 May	2 (deep water)	30	2.068	−0.0252	0.35
7 May	4	30	1.571	−0.0218	0.54
9 May	1	30	1.196	−0.0116	0.59
20 May	1	30	1.129	−0.0071	0.19
26 May	1	30	1.461	−0.0197	0.74

quency to the Chl – snow regressions for each site. When the Chl – snow regressions in Table 1 were applied to 10.1 cm mean snow depth (frequencies shown in Welch and Bergmann 1989), stations 2 and 3 had about 10-fold higher mean Chl than did station 1 (Fig. 2B).

The doubling time during the exponential growth phase for the Chl below a mean 10.1-cm snow cover at station 1 was 25.5 d, much longer than for stations 2 and 3, although there were not enough data for stations 2 and 3 to compute a rate (Fig. 2B).

Ice Algal Development Beneath Low Snow

Operationally we define "low snow" as old hoarfrost ("stucco") overlain by 1–2 cm of snow, such that the depth of snow and frost constitutes a 2- to 4-cm layer on top of the ice (Welch and Bergmann 1989). This is the minimum snow thickness generally found on thick first-year sea ice, and it is under such conditions that ice algae develop maximum biomass because the light flux there is highest.

Ice algae beneath low snow at station 1 grew exponentially from about February 10 until 26 April, peaking at only about 16 mg Chl·m^{-2}, after which the algal Chl changed little until the beginning of melt about 1 June (Fig. 2C). The time required for a doubling of ice algal Chl during this exponential growth phase was 21.9 d and the specific growth rate μ was $0.032 \cdot d^{-1}$.

Ice algae beneath low snow at station 2 also grew exponentially until late April, probably beginning about the same time in February (extrapolated back in Fig. 2C). Their growth rate (μ) was $0.072 \cdot d^{-1}$ and the doubling time was 9.7 d, about twice as fast as for algae at station 1. Maximum Chl was about 170 $mg \cdot m^{-2}$. The single set of samples obtained at station 3 in Daly Bay had the same Chl as at station 2 (Fig. 2C). A later sample at station 4 was intermediate between the two primary stations, 1 and 2 (Fig. 2C).

Effects of Amphipods on Ice Algal Biomass

Sympagic (ice-associated) amphipod densities at station 1 ranged from 100 to 800 individuals·m^{-2} from March to June, with a dry biomass of 0.5–1.7 $g \cdot m^{-2}$ (T. D. Siferd et al., unpubl.). At station 2 on Chesterfield Inlet, amphipod densities ranged from hundreds per square metre at 5–20 m depth down to 0 over deep (50–100 m) water along a transect seaward from shore. Multiple regression analysis of Chl versus amphipods and cumulative surface light for the station 2 data set, for the period 21 March to 25 April, showed that the number of amphipods summed over time for each depth sampled was barely significant (P = 0.03) and accounted for only 0.03 of the total variation, with cumulative surface light providing 0.82 of the total. We therefore conclude that amphipods had little effect on the distribution of ice algae at either station 2 or 1.

Discussion

Possible Nitrate Limitation

The data show that ice algal growth at station 2 in Chesterfield Inlet was much more rapid than at station 1 under comparable snow conditions. This result was unexpected based on our

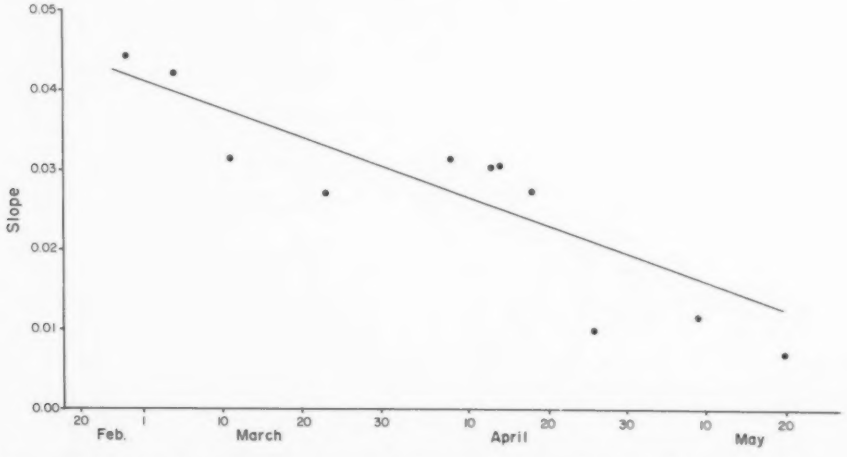

FIG. 5. Slopes of Chl – snow depth regressions (from Table 1) as a function of date where slope = −0.0620 + (0.00035) (day of year) (r^2 = 0.73).

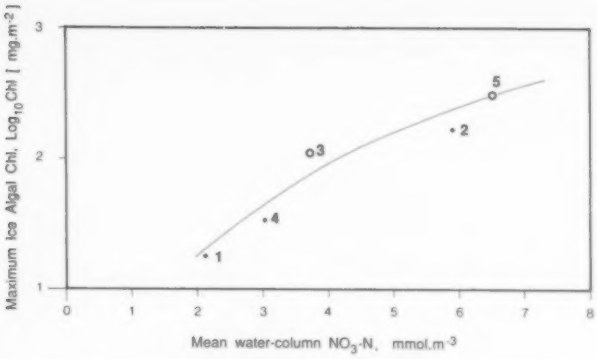

FIG. 6. Maximum development of ice algal Chl beneath low snow as a function of mean water column NO_3-N concentration during the growing season (March–May). 1 = station 1 (this study); 2 = station 2 (this study); 3 = Resolute in 1985; 4 = station 4 (this study); 5 = Resolute in 1986.

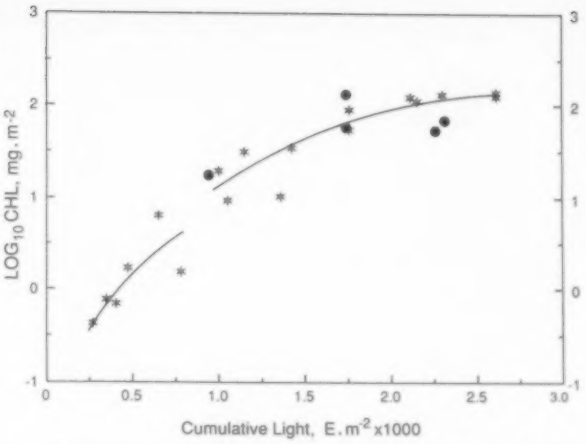

FIG. 7. Comparison of actual and predicted values of ice algal Chl as a function of cumulative surface light and snow depth for a mean snow depth of 10.1 cm. The line is the general model predicting Chl as a function of snow depth and cumulative surface light, developed from Resolute data (Welch and Bergmann 1989). * = Chl calculated from equations of Chl – snow depth at Resolute for each sampling date (from Welch and Bergmann 1989); ● = Chl calculated from equations of Chl – snow depth for stations 2 and 3 (this study).

Resolute results, where ice algal growth was synchronous and equal at all sites distributed many kilometres apart (Welch and Bergmann 1989). We could find only one difference in the variables measured, namely nitrate (NO_3-N) concentrations in the water column (Fig. 3). Nitrate was high in the unstratified water column at station 2 and low at station 1. At station 4, nitrate was intermediate (3.0 mmol·m^{-3}) the only time it was measured, and Chl was likewise intermediate (Fig. 2C; Table 1). Nitrate was always low inside Saqvaqjuac Inlet (1.7 – 2.5 mmol·m^{-3}), as was Chl (data not shown). At station 3 in Daly Bay, ice algal Chl was equal to that at station 2 (Fig. 2B and 2C; Table 1). Although nitrate was not determined, the water depth at station 3 was >100 m and through not to be isolated from offshore Hudson Bay waters by shallow sills, according to local resident M. Kukkiak (pers. comm.), suggesting that nitrate concentrations were similar to those at station 2.

We hypothesize that the cause of the nitrate differences between the sites is kelp, which is very abundant in the shallow, rocky areas typical of these coastal waters. *Laminaria solidungula* in Foxe Basin to the north takes up nitrate from the water column and begins to grow in early winter (Chapman and Lindley 1980). We suggest that, in shallow, partly enclosed basins such as station 1, kelp have removed most of the nitrate by the time the ice algae begins to grow and that continued uptake of nitrate by kelp is sufficient to keep nitrate concentrations depressed in shallow nearshore waters for the duration of the ice algal growing season. Only in deep, well-circulated basins with a large reservoir of nitrate and/or unimpeded water circulation with offshore Hudson Bay (such as station 2 on Chesterfield Inlet and possibly station 3 in Daly Bay) does the nitrate remain undepleted by kelp.

Combining the Resolute and Saqvaqjuac data, we find a positive correlation between the maximum ice algal Chl reached under low snow at each location and the mean water column nitrate concentration (Fig. 6). We assume that nitrate delivery to the ice algal community is proportional to the concentration in the water (see Cota and Horne 1989). The Saqvaqjuac data points in Fig. 6 may be slightly lower than expected compared with the Resolute points because higher air temperatures terminate the bloom at 63°N before 75°N.

Applications of the Resolute Model to the Chesterfield Inlet Area

We have used the same cumulative surface light and snow depth model developed for Resolute to predict ice algal biomass for any day and snow depth at Chesterfield Inlet. At the latitude of Chesterfield Inlet (63°N) the sun is above the horizon even at the winter solstice, but we chose 10 February to begin the light accumulation because a backwards extrapolation of the regressions in Fig. 2B indicates this as the approximate date when ice algae began to grow. To illustrate the comparison between Resolute and Saqvaqjuac, we have used algal development beneath a mean snow cover of 10.1 cm; the conclusions would be the same regardless of the snow depth frequencies used. The results (Fig. 7) show that algal biomass at station 2 is closely predicted by the Resolute model whereas Chl at station 1 falls far below the predicted values. The model predicting Chl as a function of snow depth and cumulative surface light therefore seems to apply only to locations where nitrate concentrations in the upper water column are above 5–6 mmol·m^{-3} (Fig. 6). We cannot compute a synoptic estimate for maximum ice algal biomass in the Chesterfield Inlet area of Hudson Bay because of the extreme spatial heterogeneity of both snow cover and algal growth. There were several hundred square kilometres of low snow area at Daly Bay and Chesterfield Inlet that developed about 170+ mg Chl·m^{-2} whereas the inshore, higher snow areas typified by station 1 grew an order of magnitude less Chl. On the main body of Hudson Bay seaward of the flaw lead, we expect ice algal growth to be the same as at deepwater stations 2 and 3, but we have no way of knowing this. Synoptic estimates of ice algal biomass in northwest Hudson Bay will require sampling 10–100 km offshore and remotely sensed snow depth data gathered over large areas.

Conclusions

Light, controlled primarily by snow cover, regulated ice algal biomass during the exponential growth phase in northwest Hud-

son Bay. Ice-associated amphipods have little effect on biomass accumulation rates. However, low concentrations of dissolved inorganic nitrogen in semienclosed basins inshore appear to depress growth rates far below the maxima set by light. Where nutrients are adequate, ice algal biomass beneath first-year sea ice on northwest Hudson Bay is closely predicted by the same cumulative light and snow depth model developed from Resolute data. Therefore we conclude that ice algal growth over large areas of the Canadian Arctic is predictable from cumulative surface light and snow depth.

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Evidence for Attacks by the Bathypelagic Fish *Anotopterus pharao* (Myctophiformes) on Pacific Salmon (*Oncorhynchus* spp.)

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Adult Pacific salmon (*Oncorhynchus* spp.) returning from offshore waters to spawn frequently bear a wide range of wounds and scars. One of the most common wounds is a single slash mark on the posterior third of one side of the body, running posteroventrally from near the dorsal fin at a roughly 45° angle. The evidence is reviewed for the occurrence of slash-marked salmon around the Pacific Rim over the past 30 yr. A jaw fragment removed from the wound of a slash-marked sockeye salmon (*O. nerka*) and identified as belonging to a daggertooth (*Anotopterus pharao*: order Myctophiformes), a highly modified bathypelagic fish, provides the first direct evidence for the cause of these wounds. Given the frequency of slash-marked adult salmon in coastal fisheries, *A. pharao* may be a significant cause of mortality in Pacific salmon that has previously gone unrecognized.

Le saumon du Pacifique (*Oncorhynchus* spp.) adulte qui remonte les rivières pour venir pondre, porte quantité de blessures et de cicatrices. Une des blessures les plus courantes est une entaille unique dans le tiers postérieur du corps, d'un seul côté, partant de la proximité de la nageoire dorsale selon un angle d'environ 45°, dans le sens postero-ventral. On a examiné les mentions de ces entailles sur le saumon de la région du Pacifique au cours des 30 dernières années. Un fragment de mâchoire extrait de la blessure d'un saumon rouge (*O. nerka*) a été identifiée comme provenant d'un *Anotopterus pharao* (ordre des myctophidés), un poisson bathypélagique hautement modifié, ce qui est la première indication que l'on ait de la cause de ces blessures. Vu la fréquence observée de ces entailles chez le saumon adulte, *A. pharao* pourrait être responsable d'une mortalité importante du saumon du Pacifique, alors qu'on l'ignorait totalement.

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Pacific salmon (*Oncorhynchus* spp.) with unusual slash marks have been caught in coastal and high-seas areas of the North Pacific for many years (Sano 1959a, 1959b, 1960, 1962; Jewell 1961; Fiscus 1963; Seibel et al. 1984; Gilhousen 1989; Henderson et al. 1990). In 1990, approximately 5% of adult sockeye salmon (*O. nerka*) caught in coastal waters of British Columbia bore these marks (Henderson et al. 1990), and in some years the prevalence reached 12% (Gilhousen 1989). A typical slash runs at an approximately 45° angle, occurs on only one side of the body, and appears as if made with a sharp knife (Fig. 1). The slash usually starts posterior of the dorsal fin near the lateral line and extends posteroventrally towards the ventral fin. At time of capture the condition of the wound ranges from fresh, with blood still oozing from the cut surfaces, to completely healed. In many cases the slash is deep enough to cut through the body wall and expose the internal organs (Gilhousen 1989).

The severity of the wound suggests that significant mortality may occur, but the characteristic occurrence of a single slash on only one side of the body is puzzling. We report the first direct evidence for an attack causing such a slash by a daggertooth (*Anotopterus pharao*), a bathypelagic fish (order Myctophiformes, family Anotopteridae), on sockeye salmon.

Daggertooth Biology

Anotopterus pharao is an extremely specialized member of the order Myctophiformes and the only extant member of the monotypic family Anotopteridae. It is broadly distributed throughout the world's oceans in temperate and subarctic waters (Hubbs et al. 1953). A slender, snake-like fish seldom exceeding 85 cm total length and 5 cm in diameter, its diminutive size makes it an unlikely predator on adult salmon, although its nighttime presence in surface waters does coincide with the nocturnal distribution of Pacific salmon. Judging from gillnet catches on the high seas (Neave 1959; Taylor 1959; International North Pacific Fisheries Commission Squid Drifnet Observer Program, 1989–90, unpubl. data), *A. pharao* occurs in surface (<10 m) waters of the North Pacific at night, but very little is known about its biology. Rofen (1966, p. 507) suggested that it can readily avoid collecting nets and is probably much more abundant than catch records indicate. For this

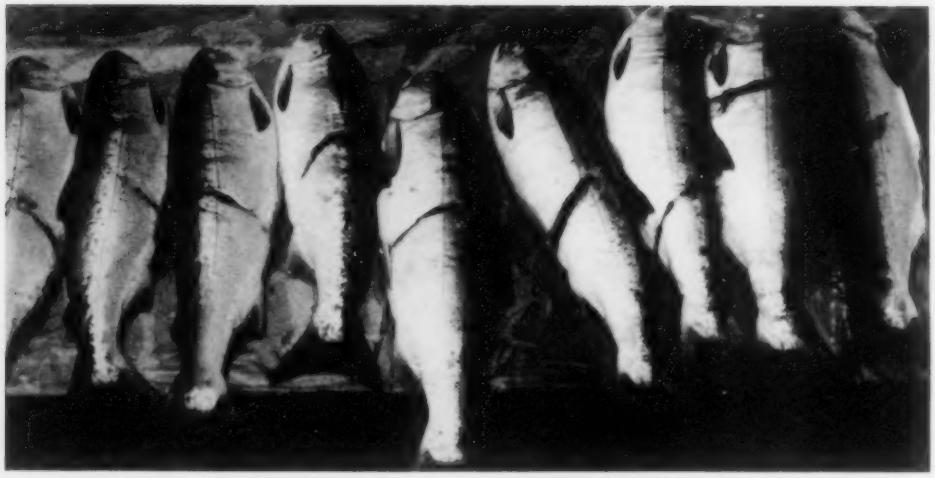


FIG. 1. Slash-marked adult sockeye salmon caught in the 1989 British Columbia coastal fishery.

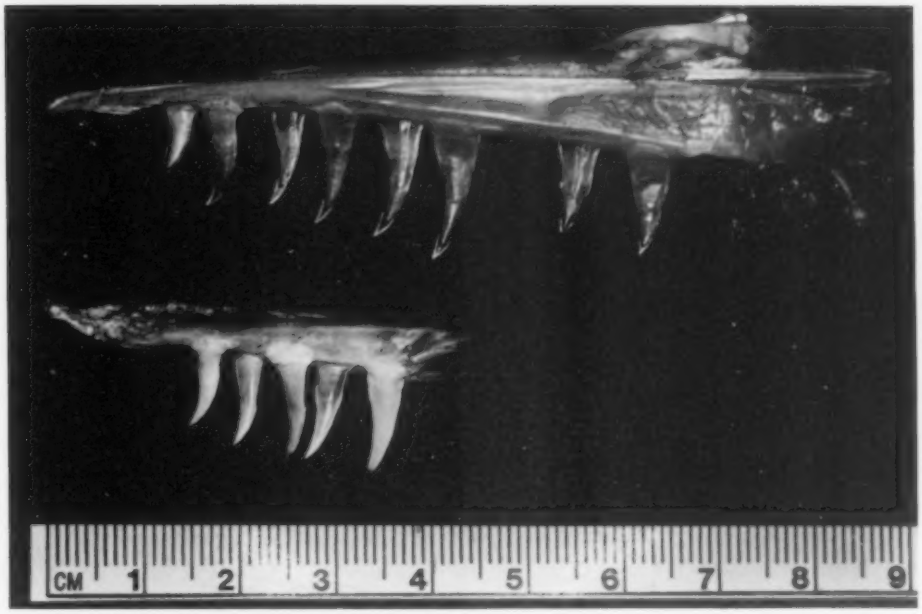
FIG. 2. Jaw fragment of the salmon predator. Anterior is to the left, and shattered bone is evident to the right of the last tooth. Both left and right maxillary bones are present, but closely parallel and not separately visible in the photograph. Note the unusual recurved nature of the teeth. Both anterior and posterior surfaces of the teeth have finely serrated edges not evident in the photograph.

reason, circumstantial evidence for its involvement in widespread attacks on the dominant members of the pelagic fish fauna in the North Pacific is of particular interest.

Materials

On about 12 August 1990, Captain P. Burgess (P.O. Box 2988, Parksville, B.C. V0R 2S0, Canada), while trolling for salmon aboard the F/V *Summer's Retreat* southwest of Cape St. James, Queen Charlotte Islands (roughly 51°N, 132°W), caught a wounded sockeye salmon with a fish jaw fragment deeply embedded in its flesh.

Captain Burgess described the wound as a fresh cut running "in the standard way" on an approximately 2.3-kg sockeye salmon. From memory, he drew the slash as extending about two thirds the depth of the fish, starting below the posterior insertion of the dorsal fin and extending down diagonally into the base of the ventral fin. He stated that when his deckhand tried to clean the fish the knife struck a hard object. They used the knife to dislodge a jaw bone with teeth from the bottom of



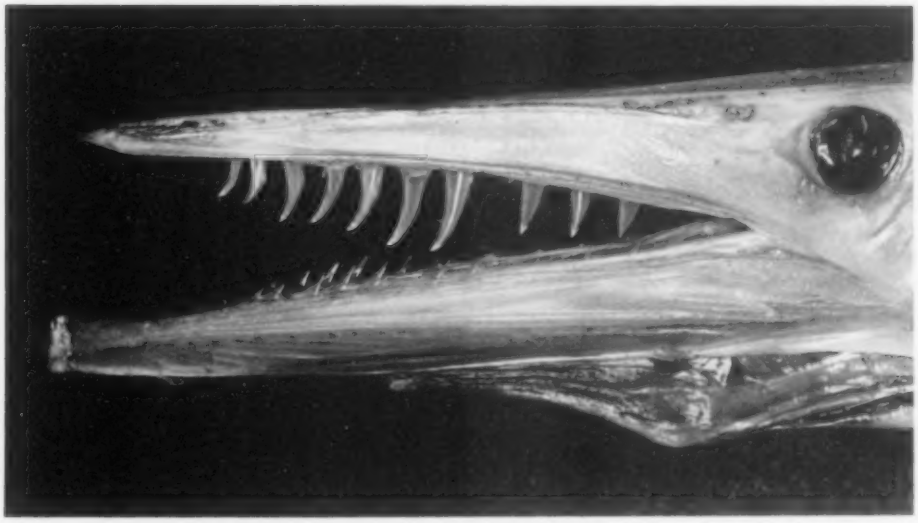


FIG. 3. *Top*: Comparison of the jaw fragment with an upper jaw of *A. pharao*, collected from a shark's stomach (University of British Columbia Ichthyological Collection No. BC 60-164); note the weak bone structure and the recurved teeth. *Bottom*: Close-up of the head of an adult *A. pharao*, (approximately 85 cm fork length) taken at 51°N, 175°W on 25 August 1956 (Royal B.C. Provincial Museum, Group C30, BC71-123).

the wound. The jaw fragment includes both left and right maxillary bones, which carry three and two large teeth, respectively (Fig. 2). Captain Burgess stated that the teeth were oriented downward and buried in the base of the fin with the 4-cm jaw fragment completely embedded in the flesh and the shattered end of the bone flush with the surface of the wound.

Identification

The remarkably reduced bone structure of the jaw and the anteriorly recurved teeth leave little doubt that the fragment is the upper jaw from *A. pharao* (Fig. 3). In addition, microscopic examination of both the anterior and posterior surfaces of the teeth reveals a series of extremely fine serrations that are also present in preserved *A. pharao* specimens held in collections of the University of British Columbia and the Royal British Columbia Provincial Museum.

Discussion

This jaw fragment is the first evidence of an attack by *A. pharao* on Pacific salmon. The report is interesting because

the identity of the organism making the characteristic slash marks has been the source of considerable conjecture. Sano (1959a, 1959b, 1960, 1962) and Gilhousen (1989) attributed these slash marks to attacks by the salmon shark (*Lamna ditropis*), but the linear nature of the single razor-like slash and the location of the wound on only one side of the body make this identification questionable. These slashes are not surface wounds, but in many cases extend deep into the body cavity (Fig. 1). In most cases there is little evidence of tissue damage other than at the wound site, and scales close to the edge of the slash are undisturbed. If they were the result of a shark attack, multiple deep lacerations would be expected on both sides of the body. In recent years the frequent occurrence of slash marks has prompted some North American fishermen to claim that they are caused by the monofilament gill nets used in the high-seas squid driftnet fishery. However, the wounds are clearly not net marks (pers. obs.).

From the location and orientation of the jaw fragment, it seems clear that the upper jaw became embedded in the pelvic girdle after cutting through the body musculature. Presumably, this provided sufficient leverage for the sockeye to shatter and tear off the jaw. Both the orientation and 4-cm depth of the wound are consistent with the characteristic diagonal slash marks found on many other sockeye salmon. although Captain Burgess did not save the salmon from which the jaw was taken, his description of the wound is consistent with others described from salmon throughout the North Pacific. Because of Captain Burgess' forthright and consistent description of events, we have no reason to question the veracity of the facts as reported to us.

Anotopterus pharao has been mentioned by Hartt (1980, p. 52) as a potential predator on juvenile salmon and a possible source of "predators scars" on salmon; however, no justification was given for including *A. pharao* in a list of salmon predators. Hartt did not examine the stomach contents of *A. pharao*, but in a telephone discussion during preparation of this report he stated to one of us (D.W.W.) that on two occasions he had observed *A. pharao* "attached" to the side of adult salmon caught by long-lines on the high seas (A. C. Hartt, 308 Alderwood St., Coupville, WA 98239, USA, pers. comm.). This further strengthens our view that *A. pharao* may be responsible for at least some of the wounds observed in coastal fisheries during the return spawning migration.

The maxillary teeth of *A. pharao*, with their unusual forward curve and finely serrated edges, are clearly adapted for cutting the flesh of prey. In preserved specimens the left and right maxillary bones are closely parallel, and the teeth are spaced such that they give the appearance of a single tooth row running down the medial line of the mouth. This arrangement of a single row of forwardly curved maxillary teeth on a strongly reduced and fragile jaw, plus the small size of the mandibular teeth, suggests that *A. pharao* usually releases its prey after attacking. It is possible that it first cripples its prey by cutting through the body musculature before attempting to feed. The morphology of the jaws is also consistent with the repeated observations of a single deep slash wound that occurs on only one side of the body of salmon.

Wounds to the opposite side of the body are not reported in the literature describing slash wounds on salmon. We have found no information on the feeding behaviour of *A. pharao*, but the fine needle-like teeth on the mandible (Fig. 3) would seem to be ill-adapted for holding strongly struggling prey because of their small size, and their retrorse orientation is in striking contrast with the orientation of the maxillary teeth. Marks left by the mandibular teeth of *A. pharao* may be relatively inconspicuous and therefore overlooked in descriptions of the slash marks, or it is possible that *A. pharao* initially attacks in such a way that the teeth of the lower jaw do not come in contact with the body. Closer examination for the presence of teeth marks on the side of the body opposite to that carrying the slash marks is clearly needed.

Conclusions

Based on a comparison of the jaw fragment with preserved specimens, we estimate that the total length of the daggertooth was roughly 80 cm. *Anotopterus pharao* is carnivorous, and its distensible stomach and unattached pectoral girdle allow it to swallow large prey (Rofen 1966). For example, two specimens of *A. pharao* measuring 75 and 82 cm caught in Davis Strait (Northwest Atlantic region) were found to contain two (28 and 30 cm in length) and three (unmeasured) *Paralepis coregonoides* (Postolakii 1962). Nevertheless, a 2.3-kg maturing sockeye salmon is almost certainly too large for an 80-cm *A. pharao* to swallow, and the loss of much of the upper jaw indicates that attacking large prey is not without risk. However, *A. pharao* may be capable of feeding successfully on smaller salmon of size similar to that of the prey reported by Postolakii (1962). As up to 12% of adult sockeye salmon returning to British Columbia waters each year bear slash marks, the potential significance of *A. pharao* as a cause of mortality for juvenile Pacific salmon therefore needs to be evaluated.

Acknowledgments

We thank Captain P. Burgess and the crew of the F/V *Summer's Retreat* for bringing the jaw to our attention and for their forbearance with our repeated questions. We also thank Mr. R. Carveth and Drs. A. Peden and N. J. Wilimovsky for provision of reference material from their research collections, Mr. A. C. Hartt for sharing his field observations on *Anotopterus*, and Mr. E. Warneboldt for his expert photography.

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Abundance, Growth, and Production Estimation of the Blue Mussel *Mytilus edulis* on Moored Navigation Buoys in the Estuary and Northwestern Gulf of St. Lawrence[1]

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Ardisson, P.-L., and E. Bourget. 1991. Abundance, growth, and production estimation of the blue mussel *Mytilus edulis* on moored navigation buoys in the Estuary and northwestern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 48: 2408–2419.

Production of *Mytilus edulis* was estimated from measurements of recruitment, growth, and abundances. The study is based on (1) yearly samplings carried out between 1975 and 1985 on 161 navigation buoys moored each year in the Estuary and Gulf of St. Lawrence and (2) monthly production estimates in a reference region in 1987. The relationships between production and maximum size, biomass, mean weight per individual, and abundance were calculated for this reference region. Maximum size and biomass were the parameters best reflecting production. Abundance and production estimates showed that the Gaspé Peninsula and the western North Shore zones were the most productive ones. The density-dependent mortality of individuals in crowded even-aged populations (self-thinning) was studied in the baie de Gaspé, the region showing the highest abundance and growth rate of *Mytilus* in the system. The slope of this relationship varied depending on initial density and age classes considered. These results, when compared with the theoretical value of the self-thinning model, suggest that the biomass observed on the buoys and the production estimates derived from them correspond to near-maximal values

La production de *Mytilus edulis* a été estimée à partir d'observation sur le recrutement, la croissance et les abondances. L'étude est basée sur (1) des échantillonnages annuels effectués entre 1975 et 1985 sur 161 bouées de navigation, mouillées annuellement dans l'estuaire et le golfe du Saint-Laurent, et (2) des estimations de production mensuelles dans une région témoin en 1987. Les relations entre la production et la taille maximale, la biomasse, le poids moyen par individu et l'abondance, sont calculées pour cette région témoin. La taille maximale et la biomasse sont les paramètres reflétant le mieux la production. Les estimations de production montrent que la Péninsule Gaspésienne et la région ouest de la Côte Nord sont les zones les plus productives. La mortalité dépendante de la densité dans des populations du même âge («self-thinning»), est étudiée dans la région montrant les plus fortes abondances et les plus forts taux de croissance dans le système, la baie de Gaspé. Le pente de cette relation varie selon la densité initiale et les classes d'âge. Ces résultats, comparés à la valeur théorique du modèle «self-thinning», suggèrent que les biomasses sur les bouées ainsi que les estimations de production en découlant correspondent à des valeurs quasi-maximales.

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Secondary production of littoral, filter-feeding invertebrates results from the interaction of many physical and biological factors. Among these, physiological stress due to air exposure, salinity fluctuations, or mud accumulation (Dare 1976; Bourget 1983), predation and competition (Dare 1976; Edwards et al. 1982; Sousa 1985), genetic and physiological traits (Koehn et al. 1976; Koehn and Bayne 1989), food quality and quantity (Fréchette and Bourget 1985a, 1985b; Riisgård 1988), larval dispersal (Mann 1988), and settlement and recruitment dynamics (Connell 1985; Possingham and Roughgarden 1990; Sutherland 1990) accounts for much of the variability in abundance and growth of littoral fauna. By contrast, organisms inhabiting continuously submerged suspended substrata experience decreased physiological stress and increased access to food while escaping from littoral predators (Poirier and Myrand 1982; Dardignac-Corbeil 1986; Mallet and Carver 1989). This is reflected by rapid growth and high survival rate (Rodhouse et al. 1984a, 1984b). Hence, estimates obtained from suspended substrata represent potential rather than realized production estimates of the species.

There exist very few studies of benthic secondary production at large spatial scales. This is mainly due to the difficulty of obtaining comparable samples over wide regions. Indeed, sampling littoral fauna over large distances is in most cases impractical and costly. The use of a large number of suspended collectors simultaneously can help to overcome this problem (see Fradette and Bourget 1980, 1981). Furthermore, mooring uniform artificial substrata in different environments makes possible direct comparisons without the variability associated with substratum type (Schoener 1982; King et al. 1990).

The present paper represents such an attempt to examine production at the scale of hundreds of kilometres using the blue mussel *Mytilus edulis*, a dominant shore invertebrate, in a large semi-enclosed marine system, the Estuary and Gulf of St. Lawrence. The objectives of the study are to (1) characterize the

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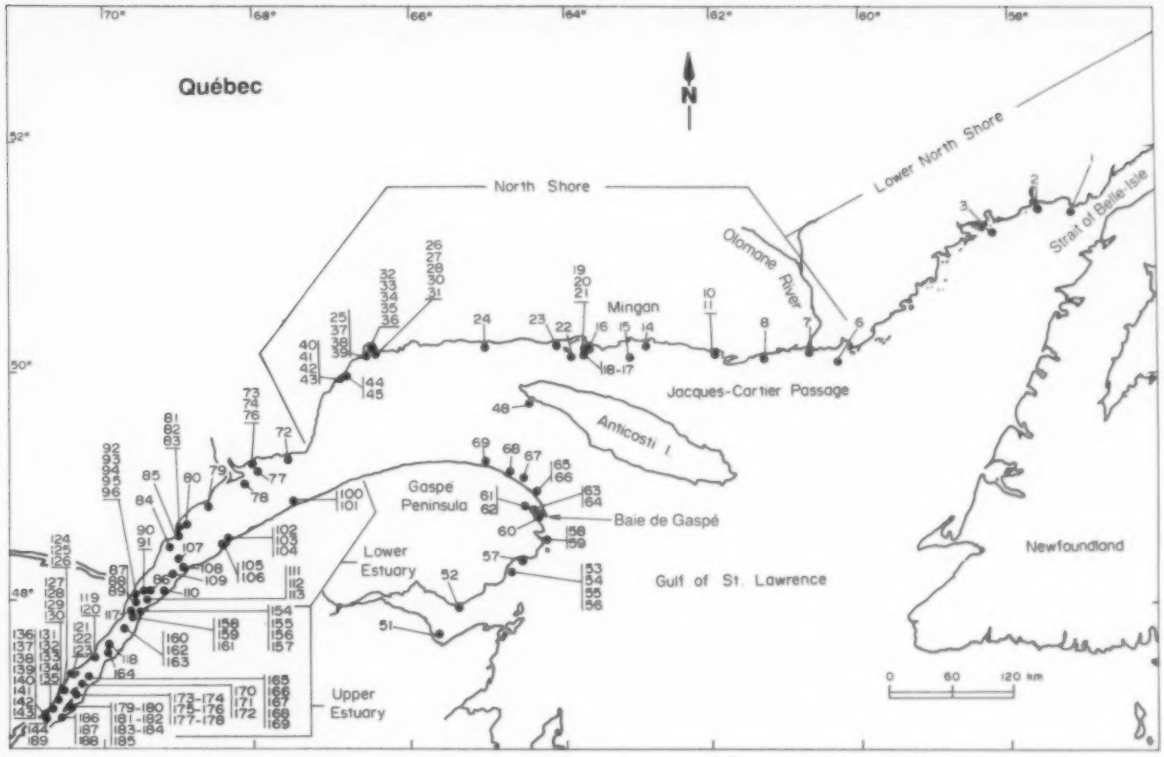

FIG. 1. Position of collectors moored in the Estuary and northwestern Gulf of St. Lawrence.

spatial variability in recruitment and growth of juvenile (<1 yr old) mussels at the scale of the Estuary and Gulf and (2) determine the reliability of various mussel indices to estimate production. The approach used was first to measure maximum production at low, intermediate, and high mussel densities in a reference region and then to relate these production values to biomass, mean weight per individual, abundance, and maximum size values obtained for different regions. The study is based on an extensive sampling program of *M. edulis* carried out over an 11-yr period from 1975 to 1985. Samples were obtained from natural mussel populations growing on suspended collectors moored along the shores of the study area. Since these organisms are suspension-feeders, they are good indicators of the growth conditions prevailing in the surface water layer.

Materials and Methods

Collectors

Navigation buoys, moored by Transport Canada from May through November of each year along the shores of the Estuary and the northwestern Gulf of St. Lawrence (Fig. 1), were used as collectors (see Fradette and Bourget 1980, 1981; Ardisson et al. 1990). During winter, the buoys were scraped and painted. The paint used contained no antifouling agents and, as a result, the buoys moored each spring had clean surfaces apparently offering little or no resistance to larval settlement. Throughout the annual 7-mo immersion period, the buoys were colonized by sessile organisms, presumably according to the relative abundance of their planktonic larvae. Since the buoys were moored and retrieved each year in a short period of time (about 2 wk), little or no seasonal differences in abundance among regions were introduced.

Sampling of Collectors

In accordance with the method of Fradette and Bourget (1980, 1981) and Ardisson et al. (1990), one quadrat sample of 0.01 m^2 was taken from the area of maximum mussel abundance (determined by visual inspection) on each buoy. Since the mussel distribution on buoys was most often patchy, sampling the area of maximum abundance was the most practical way to obtain comparable data among buoys. The only alternative would have been to select randomly a large number of quadrats on each buoy, which would have generated an unmanageable number of samples. One hundred and sixty-one collectors were sampled from mid-November to mid-December from 1975 to 1985 (except in 1978 and 1979). The information thus obtained at the scale of the Estuary–Gulf system allowed us to identify sites of maximum recruitment and growth. One of those sites, the baie de Gaspé, was selected for a detailed study of production during 1987.

In baie de Gaspé, quantitative sampling (0.01-m^2 quadrats) was carried out in situ, using SCUBA, on two buoys (Nos. 63 and 64, Fig. 1) 300 m apart. On each buoy, populations of three different initial densities, low, intermediate, and high (corresponding to ~7000, 9000, and 15 000 ind·0.01 m^{-2}, respectively), were first sampled on 6 August 1987. The relative homogeneity of the mussel bed on the buoys limited the

number of initial densities sampled. Temporal changes in abundance, biomass, and size of these populations were estimated from repeated samplings on the buoys on 8 September, 13 October, and 2 November 1987. Underwater, sampling was carried out manually by scraping the surface of the buoys. Therefore, before being collected, each 0.01-m^2 quadrat was enclosed using a net with a 50-μm mesh size in order to recover the sample without mussel losses. Sampling sites were marked using magnets to avoid resampling. Five replicate samples per initial density were collected on each buoy and sampling date.

Laboratory Procedure

Samples were sorted and individuals counted and weighed (wet weight). Biomass (dry weight) estimates were obtained using a wet weight to shell-free dry weight conversion index (see Fredette and Bourget 1980: *M. edulis* = 0.09). The mussel length (the maximum distance between umbo and posterior margin) was measured using a vernier caliper (precision 0.05 mm), and the shell length of the largest individual (hereafter called maximum size) was recorded.

Because settlement was quasi-continuous during the period of study, samples collected from the buoys moored in baie de Gaspé in 1987 were separated into four size classes to improve the accuracy of production estimates. Size classes corresponding to ⩾10.1, 5.1–10.0, and ⩽5.0 mm shell length were separated on the basis of their width and height using sieves of 4.0-, 2.0-, and 0.18-mm mesh size. Organisms ⩾10.1 mm were further separated, using a vernier caliper, into two size classes (10.1–15.0 and ⩾15.1 mm). All organisms were counted except those ⩽5.0 mm which, due to their large number, were subsampled by the method of Elliott (1977). For each size class, wet weight was converted to dry weight using the conversion index of Fradette and Bourget (1980) (see above).

Data Analysis

The yearly efficiency of buoys as collectors was evaluated by means of the mean interannual biomass potential index. This index is the ratio of each yearly biomass value observed on a given buoy to the maximum biomass value observed on the same buoy during the entire period of study (w/w_{max}). After an arcsine transformation of the w/w_{max} values, the mean and the median were then computed and plotted by region. The arcsine transformation, measured in degrees, is especially appropriate to percentages and proportions and prevents the variance from being a function of the mean (Sokal and Rohlf 1981).

The production estimates (P) for each initial population density on the buoys from baie de Gaspé were determined from monthly changes in mean abundances (N) and the average weight per individual ($\bar{\omega}$) by the method of Crisp (1984). The total production was obtained as follows:

$$(1)\quad P = \sum_{t=0}^{t=1} N_0\, d\bar{\omega} + \sum_{t=1}^{t=2} N_1\, d\bar{\omega} + \sum_{t=2}^{t=3} N_2\, d\bar{\omega} + \ldots + \sum_{t=n-1}^{t=n} N_{n-1}\, d\bar{\omega}.$$

Each term represents the change of total biomass ($N\Delta\bar{\omega}$) during short time intervals for each age class. To account for the nearly continuous recruitment, we assumed that the four size classes ⩽5.0, 5.1–10.0, 10.1–15.0, and ⩾15.1 mm corresponded approximately to each of the first 4 mo of growth of the organisms. The observed increase in shell length with time show that these approximations were realistic. The production estimates were then related to various indices (maximum size, biomass, mean individual weight, and abundance) obtained in November for each initial population density. Geometric mean (GM) regression model of the form $Y = u + vX$ (Ricker 1973) was used here because both Y and X variables were subject to natural variability. The mussel indices best fitting production estimates in baie de Gaspé were selected as mussel production estimators in the other regions of the system.

The effect of intraspecific competition on growth was studied in baie de Gaspé by examining the temporal changes in the relationship between log density and log biomass in crowded even-aged populations. Mortality resulting from intraspecific competition associated with high population densities (self-thinning) can be expressed as

$$(2)\quad B = CN^{\gamma}$$

where B is biomass (grams), N is density (number of individuals per unit area), C is a constant, and γ (taking ideally a value of -0.5) is the slope of the regression line (see Westoby 1977, 1984; Weller 1987a). This relationship is basic to the population dynamics of permanently attached organisms (Yoda et al. 1963; Moore 1977; White 1981). Initially applied to a large range of plant species in natural as well as experimental conditions, the "self-thinning rule" was also applied successfully to certain marine algal and benthic invertebrate species (Cousens and Hutchings 1983; Begon et al. 1986; Hughes and Griffiths 1988). This empirical relationship, largely accepted today although little understood (see Osawa and Sugita 1989; Weller 1990; Lonsdale 1990), establishes that the regression coefficient of -0.5 represents a final, stable trajectory in the growth process, as well as a limit condition of the maximal combination of average density and biomass, hence production, for a given population. Recent developments, however, have pointed out that γ does not take a constant value, but rather a range of values mainly depending on the growth allometry of species (Weller 1987b; Norberg 1988). Hughes and Griffiths (1988) showed that self-thinning exponents estimated for mussels can be explained by the competitive occupation of substratum, allometric growth, and the configuration of packing. Furthermore, Fréchette and Lefaivre (1990) showed that under situations of space limitation, multilayer packing, substrate heterogeneity, and allometric growth modify the thinning sope. In the absence of an adequate evaluation of the multilayered packing, the theoretical value of γ was considered. The GM regression model of Ricker (1973) was used here because both density and biomass were subject to natural variability and were in different units of measurement. Since, in the GM regression model, testing the slope against a given theoretical value is inappropriate (Sokal and Rohlf 1981, p. 550), only the 95% confidence limits were used to determine if the resulting slope value v (equivalent to the slope γ) differs from -0.5, the value predicted by the self-thinning model.

Results and Discussion

Buoys as Collectors

In most years, the mean biomass values observed on collectors were low compared with the maximum biomass values observed on these same collectors during the entire 1975–85 period (Fig. 2). Considering that sampling was carried out in the area of maximum abundance of the mussel bed on

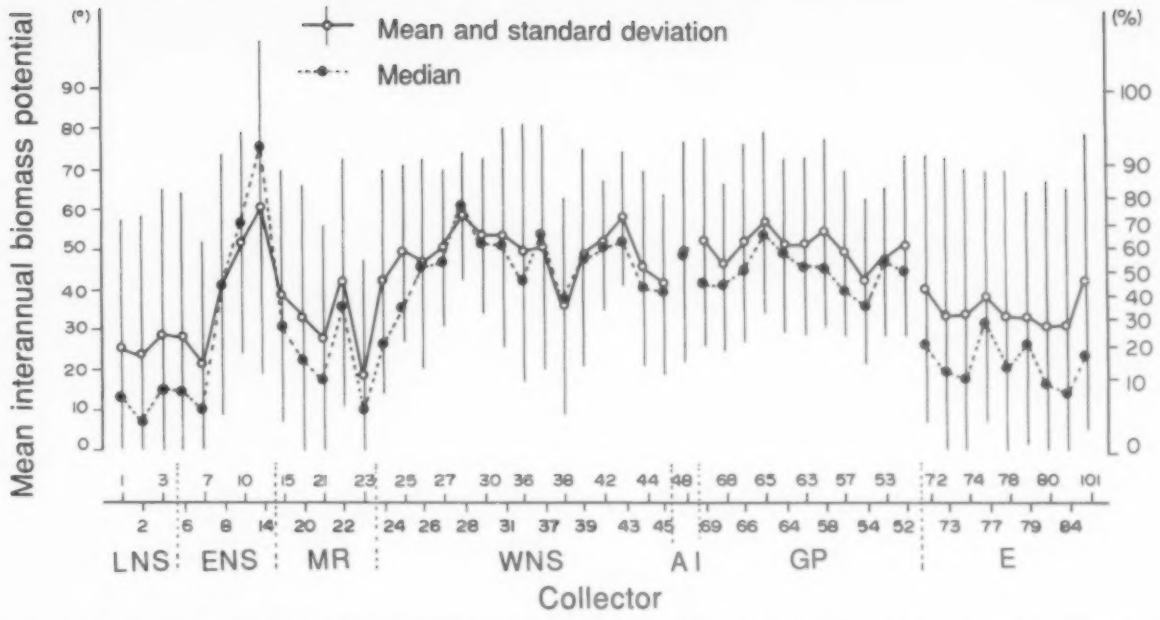

FIG. 2. Mean interannual biomass potential of *M. edulis* observed on each collector during the period 1975–85. LNS, Lower North Shore; ENS, Eastern North Shore; MR, Mingan Region; WNS, Western North Shore; AI, Anticosti Island; GP, Gaspé Peninsula; E, Estuary. Ordinate axes represent arcsine-transformed data expressed, respectively, in degrees (left) and precentages (right) (see explanation under Data Analysis). Gulf stations are presented first. All stations are ordered from the east to the west except for those of the Gaspé Peninsula which are listed from the north to the south.

each buoy, this suggests that, during the first months of growth on initially clean suspended collectors, mussels rarely saturated the available space even at maximum density. Consequently, the observed initial recruitment probably reflected the larval abundance in the environment. The undersaturation of the substratum was particularly evident on collectors situated along the Lower North Shore, the Mingan region, and the Lower Estuary.

Variability in Abundance and Biomass

Colonization by *M. edulis* occurred every year and was widespread within the Estuary–Gulf system. In the Estuary, mussels were occasional and their abundance low. Collectors with no mussels were only observed in this area (29% of all collectors moored in the Estuary). These collectors were located in the Upper Estuary and near the mouth of the Saguenay Fjord where the influence of fresh water is dominant (see Therriault and Levasseur 1985). Abundances were greater in both the Gaspé Peninsula and the western North Shore regions than elsewhere in the system (Fig. 3A and 3B). In each of these regions the biomass variation among collectors matched the variation in abundance, except in the southern part of the Gaspé Peninsula (collectors 52–58) where low mussel densities were associated with high biomass values. Indeed, the mean weight per individual was higher in this region than elsewhere in the system.

There was a strong variability in the biomass of *M. edulis* at intermediate and small spatial scales. For example, the spatiotemporal variability of biomass along the Gaspé Peninsula can be characterized by a double entry matrix in which each line represents the temporal variability of each collector and each column the spatial variability of different collectors for particular years (Table 1). The interannual variability in biomass for single collectors (cv) ranged between 45.7 and 63.4%. On the other hand, the variability among collectors within the same year varied between 28.1 and 68.2%.

Recruitment and biomass varied largely across the study area. Results shown in Fig. 3A and 3B indicate regions particularly favourable for recruitment: the northern Gaspé Peninsula region (10^4 ind·0.01 m^{-2}), characterized by high biomass (10 g·0.01 m^{-2}), and others (southern Gaspé Peninsula) which although characterized by lower recruitment (10^3 ind·0.01 m^{-2}), showed biomass values as high as those of the northern Gaspé Peninsula. Finally, there were regions where mussel abundance as well as the biomass were particularly low (e.g. the Mingan region: $1–10^2$ ind·0.01 m^{-2} and $10^{-1}–1$ g·0.01 m^{-2}, respectively). These values, obtained on suspended collectors, probably differ from those likely to be found in the littoral zone, but indicate maximum possible values for abundance and biomass in the system. Given the offshore location of collectors, these values are probably applicable to areas with a rectilinear shore contour. Along indented shores, within bays and sheltered regions, biomass and abundance levels may differ from those observed in this study. In sheltered regions, the relative stability of the water column and greater concentrations of organic matter could lead to higher levels of biomass and production than in more exposed waters. Given the large size of the region considered, the biomass and abundance levels observed in this study constitute a sound base for meso- and megascale comparisons.

Production Estimates in baie de Gaspé

Secondary production (P) within a given period of time results from increases in weight associated with growth, weight

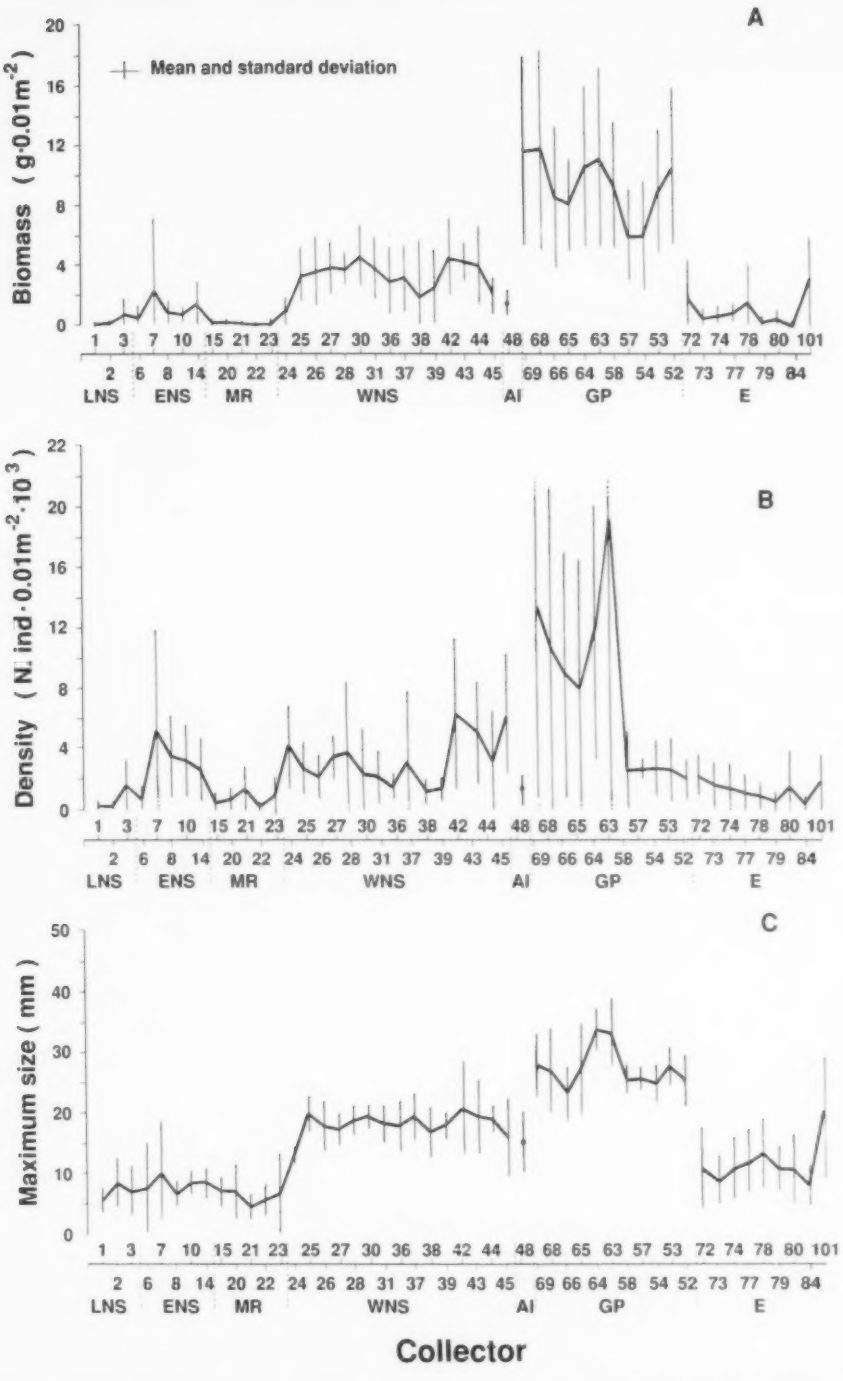

FIG. 3. Mean interannual spatial variation of mussel abundance and growth on collectors moored in different regions of the system during the period 1975–85. (A) maximum biomass; (B), maximum density; (C), maximum size (shell length of the largest individual. LNS, Lower North Shore; ENS, Eastern North Shore; MR, Mingan Region; WNS, Western North Shore; AI, Anticosti Island; GP, Gaspé Peninsula; E, Estuary.

TABLE 1. Spatiotemporal variability of biomass (dry weight, g·0.01 m^{-2}) observed on the collectors moored in the Gaspé Peninsula region during the period 1975–85 (—, 1978, 1979, 1982, collectors and years not sampled).

Buoy No.	Year								$\bar{X}$	s	cv(%)
	1975	1976	1977	1980	1981	1983	1984	1985			
69	10.00	—	—	—	—	8.51	21.05	7.08	11.66	6.37	58.07
68	10.00	10.92	24.05	3.62	6.64	7.48	18.07	14.48	11.91	6.68	57.88
66	8.66	—	4.80	2.95	5.71	7.63	15.25	15.01	8.57	4.85	58.56
65	—	8.06	4.48	—	4.87	10.70	12.54	—	8.13	3.54	45.66
64	—	5.49	10.58	5.07	6.72	16.59	18.84	11.54	10.69	5.42	52.53
63	5.78	8.62	19.73	4.24	6.48	14.71	18.79	11.62	11.26	5.99	54.86
58	6.33	—	—	—	—	7.21	15.82	8.63	9.50	4.32	48.33
57	—	2.38	4.28	4.67	4.40	11.45	7.55	8.31	6.15	3.10	52.21
54	4.18	6.41	4.35	3.71	2.01	8.49	13.84	5.14	6.02	3.67	63.37
53	4.07	10.07	17.80	6.61	5.33	9.95	9.29	9.30	9.05	4.19	47.79
52	—	—	19.45	—	5.02	9.45	10.46	9.37	10.75	5.32	51.73
$\bar{X}$	7.00	7.42	12.17	4.41	5.24	10.20	14.68	10.05			
s	2.56	2.92	8.08	1.20	1.47	3.04	4.37	3.12			
cv(%)	37.83	40.79	68.25	28.15	28.8	30.47	30.43	31.87			

TABLE 2. Temporal variation in numbers, weight, and size of *M. edulis* recruits observed at three initial population densities on two navigation buoys moored in baie de Gaspé (Qué.) during summer and autumn 1987 (—, missing value).

Date	Biomass (dry weight, g·0.01 m^{-2})	Abundance (no.·0.01 m^{-2})	Mean weight per individual (g)	Maximum weight per individual (g)	Maximum size (mm)
Density 1 (high)					
6 Aug.	0.701	14846	0.00005	0.002	6.1
8 Sept.	3.468	21287	0.00016	0.022	15.5
13 Oct.	8.025	11590	0.00069	0.125	22.8
2 Nov.	12.707	11772	0.00108	0.216	30.2
Density 2 (intermediate)					
6 Aug.	—	—	—	—	—
8 Sept.	2.283	8737	0.00026	0.018	12.6
13 Oct.	5.506	6436	0.00086	0.061	19.9
2 Nov.	9.632	9336	0.00103	0.121	25.5
Density 3 (low)					
6 Aug.	0.262	7458	0.00004	0.001	5.3
8 Sept.	0.599	2776	0.00022	0.012	11.1
13 Oct.	1.701	3658	0.00047	0.042	15.4
2 Nov.	5.173	10402	0.00050	0.059	18.0

losses, and mortality (natural or otherwise) over short time intervals. Each term in Eq. 1 (see above) involves two important parameters influencing production: the number of individuals (N) and the average weight per individual ($\bar{\omega}$). While the number of individuals per unit area (abundance) is influenced by the number of larvae settled and losses following settlement, the mean individual weight is influenced by growth.

By the end of the mooring period of buoys in early November, the number of recruits was to the order of 10^4·0.01 m^{-2}, irrespective of the initial density. Further, by this date, in spite of the prevailing sea surface temperature (~5°C: Gregory et al. 1988), mussels showed no sign of growth arrest (see Table 2).

The presence of individuals ≥5.1 mm in size at the beginning of August suggests that settlement occurred during the previous month. Observations carried out in recent years in baie des Chaleurs and Îles-de-la-Madeleine indicate that settlement in this area begins in late June (P. Bergeron, Biorex G. C. Inc., 119-2065 Blvd. Charest O, Ste-Foy (Québec), pers. comm.). Thus, the organisms collected in August could be up to 4–5 wk old. The total production estimates and maximum growth rate would therefore correspond to the first 17 wk of sedentary life.

Density 1 (initial density ~7000 ind·0.01 m^{-2}) had the highest total production estimate: 88.0 g·0.01 m^{-2}·5 mo^{-1} ($P/\bar{B}$ ratio = 14.1). The intermediate value corresponded to density 2 (initial density ~9000 ind·0.01 m^{-2}) with 47.3 g·0.01 m^{-2}·5 mo^{-1} ($P/\bar{B}$ ratio = 8.1) and the lowest to density 3 (initial density ~15 000 ind·0.01 m^{-2}) with 22.9 g·0.01 m^{-2}·5 mo^{-1} ($P/\bar{B}$ = 11.8) (Tables 2 and 3).

These production estimates, obtained at the site showing the highest mussel abundance and growth rates of the whole system during the period 1975–85, are, in absolute terms, particularly high. There exist, however, few data in the literature with which to compare these estimates. Southgate and Myers (1985) observed a maximum biomass value of adult mussels on gas platforms south of Ireland of 13.9 kg·m^{-2} at 4 m depth (1.25 kg·m^{-2}, according to the wet weight to shell-free dry weight index calculated by Fradette and Bourget (1980)). This value is near the maximum biomass observed in baie de Gaspé in November (12.7 g·0.01 m^{-2}) (Table 3). The biomass values reported by Beukema (1976) for *M. edulis* in the intertidal zone are of the order of 6.2 g dry weight·m^{-2} (all size classes pooled), which are well below the mean maximum values observed in this study. In the littoral regions, various authors

TABLE 3. Estimates of production of a *M. edulis* population recruited on navigation buoys during summer and autumn 1987 in baie de Gaspé (Qué.)

I Date	II Cohort	II′ Size class (mm)	III Abundance per size class (No.·0.01 m^{-2})	IV Mean weight per individual ϖ (g)	V Weight increment $\Delta\varpi$ (g)	VI Mean value of N during Δt	VII Production increment $N\Delta\varpi$ (g·0.01 m^{-2})
Density 1 (high)							
~25 June	0	<5.0	0	0	—	—	—
6 Aug.		5.1–10.0	24.4	0.00104	0.00104	12.2	0.013
8 Sept.		>10.1	64.5	0.01568	0.01464	44.4	0.651
						$\sum_{0}^{1} N\Delta\varpi$	0.664
~25 June			0	0	0		
6 Aug.	1	<5.0	14822	0.00005	0.00005	7411.0	0.371
8 Sept.		5.1–10.0	807	0.00255	0.00250	7814.5	19.535
13 Oct.		10.1–15.0	228	0.01388	0.01133	517.5	5.863
2 Nov.		>15.0	172	0.04379	0.02991	200.0	5.982
						$\sum_{1}^{2} N\Delta\varpi$	31.751
6 Aug.			0	0			
8 Sept.	2	<5.0	20415	0.00004	0.00004	10207.5	0.408
13 Oct.		5.1–10.0	586	0.00321	0.00317	10505.5	33.287
2 Nov.		10.1–15.0	225	0.01407	0.01086	405.5	4.404
						$\sum_{2}^{3} N\Delta\varpi$	38.099
8 Sept.			0	0			
13 Oct.	3	<5.0	10707	0.00006	0.00003	5353.5	0.161
2 Nov.		5.1–10.0	469	0.00314	0.00308	5588.0	17.211
						$\sum_{3}^{4} N\Delta\varpi$	17.372
13 Oct.			0	0			
2 Nov.	4	<5.0	10906	0.00006	0.00003	5453.0	0.164
						Total production	88.050
Density 2 (intermediate)							
~25 June	0	<5.0	0	0	—	—	—
6 Aug.		5.1–10.0	33.7[a]	0.00441[a]	0.00441[a]	16.8[a]	0.074[a]
8 Sept.		10.1–15.0	67.4	0.00882	0.00441	50.5	0.223
13 Oct.		>15.0	37	0.03235	0.02353	52.2	1.228
						$\sum_{0}^{1} N\Delta\varpi$	1.525
~25 June			0	0			
6 Aug.	1	<5.0	7430[a]	0.00008[a]	0.00008[a]	3715[a]	0.297[a]
8 Sept.		5.1–10.0	564	0.00261	0.00253	3997	10.112
13 Oct.		10.1–15.0	152	0.01399	0.01138	358	4.074
2 Nov.		>15.0	122	0.03564	0.02165	137	2.966
						$\sum_{1}^{2} N\Delta\varpi$	17.449
6 Aug.			0	0			
8 Sept.	2	<5.0	8106	0.00008	0.00008	4053.0	0.324
13 Oct.		5.1–10.0	513	0.00336	0.00328	4309.5	14.136
2 Nov.		10.1–15.0	211	0.01393	0.01057	362.0	3.826
						$\sum_{2}^{3} N\Delta\varpi$	18.286
8 Sept.			0	0			
13 Oct.	3	<5.0	5734	0.00008	0.00008	2867	0.229
2 Nov.		5.1–10.0	522	0.00312	0.00304	3128	9.510
						$\sum_{3}^{4} N\Delta\varpi$	9.739
13 Oct.			0	0			
2 Nov.	4	<5.0	8451	0.00007	0.00007	4225.5	0.296
						Total production	47.295

TABLE 3. (*Concluded*)

I Date	II Cohort	II′ Size class (mm)	III Abundance per size class (No.·0.01 m^{-2})	IV Mean weight per individual ϖ (g)	V Weight increment $\Delta\varpi$ (g)	VI Mean value of N during Δt	VII Production increment $N\Delta\varpi$ (g·0.01 m^{-2})
Density 3 (low)							
~25 June	0	<5.0	0	0	—	—	—
6 Aug.		5.1–10.0	5	0.00086	0.00086	2.5	0.002
8 Sept.		10.1–15.0	7.83	0.00860	0.00774	6.4	0.050
13 Oct.		>15.0	1	0.03042	0.02182	4.4	0.096
						$\sum_{0}^{1} N\Delta\varpi$	0.148
~25 June			0	0			
6 Aug.	1	<5.0	7453	0.00005	0.00005	3726.5	0.186
8 Sept.		5.1–10.0	160	0.00217	0.00212	3806.5	8.070
13 Oct.		10.1–15.0	53.9	0.01336	0.01119	107.0	1.197
2 Nov.		>15.0	27.1	0.03067	0.01731	40.5	0.701
						$\sum_{1}^{2} N\Delta\varpi$	10.154
6 Aug.			0	0			
8 Sept.	2	<5.0	2608	0.00007	0.00007	1304.0	0.091
13 Oct.		5.1–10.0	191	0.00305	0.00298	1399.5	4.171
2 Nov.		10.1–15.0	190	0.01297	0.00992	190.5	1.890
						$\sum_{2}^{3} N\Delta\varpi$	6.152
8 Sept.			0	0			
13 Oct.	3	<5.0	3412	0.00008	0.00008	1706.0	0.136
2 Nov.		5.1–10.0	429	0.00325	0.00317	1920.5	6.088
						$\sum_{3}^{4} N\Delta\varpi$	6.224
13 Oct.			0	0			
2 Nov.	4	<5.0	9756	0.00004	0.00004	4878.0	0.195
						Total production	22.873

[a]Estimated from the information available from other cohorts.

(e.g. Burke and Mann 1974; Dare 1976; Robertson 1979; Howe et al. 1988) observed *M. edulis* production values fluctuating between 1.2 $g \cdot m^{-2} \cdot yr^{-1}$ and 2.9 $kg \cdot m^{-2} \cdot yr^{-1}$ (all size classes pooled) which are below those observed in this study. The annual turnover of biomass ($P/\overline{B}$ ratios) suggested by Waters (1969) and Parsons et al. (1984) for different macrobenthic species (between 2.5 and 6 with a mode of 3.5) was estimated from values observed during the whole life of a cohort. These results, however, can hardly be compared with the $P/\overline{B}$ observed for populations consisting of juveniles colonizing suspended substrata. Physical stress, topography, and intense predation can probably explain the low biomass, production, and $P/\overline{B}$ ratios observed in the littoral zone.

No data on mussel production exist for the study area. however, the high values of abundance, maximum growth, and production estimates observed in the Gaspé Peninsula area are consistent with the available oceanographic and primary productivity data (Sevigny et al. 1979; de Lafontaine et al. 1984), identifying this area as one of the most productive zones of the Estuary–Gulf system. According to Fradette and Bourget (1981), who calculated an index of food supply on the basis of published data of mean residual current speed and concentration of chlorophyll *a*, the Lower Estuary and the Gaspé coast appear to be the most productive zones likely to sustain active growth of planktivorous populations. However, phytoplankton concentrations in these areas are spatially and temporally heterogeneous (Demers et al. 1989; de Lafontaine et al. 1991; Therriault et al. 1990), so more detailed studies are necessary to evaluate the mussel productivity at smaller spatial scales than those used in this study.

Indices of Production

Maximum size and biomass were the indices best reflecting production (Table 4). The close relationship observed between production and maximum size ($R^2 = 0.977$) is not surprising because, in our study, maximum size corresponds also to maximum growth rate, all buoys being moored for the same period of time. Evidence from the literature for similar relationships is scarce and inconclusive. Nielsen (1985), in an experimental study on juvenile *M. edulis* (<1 yr old), observed a strong correlation between the average increase of shell-free dry weight (net production) and the average increase in shell length during short periods of time (4–12 d). Hilbish (1986), studying an intertidal *M. edulis* population, did not observe this relationship, but found a decoupling of shell growth and tissue growth over a longer period of time, pointing to the limitations of using shell growth alone in estimating production in marine bivalves. Biomass, in contrast, has long been recognized as a reliable predictor of production (Rigler and Downing 1984; Plante and Downing 1989).

The equations $Y = 0.0135\ MS^{2.557}$ and $Y = 1.953\ B^{1.466}$ relating, respectively, maximum size (MS) and biomass (B) to

TABLE 4. Relationships between the production estimates (P) obtained at three different initial population densities and maximum size (MS), biomass (B), mean weight per individual (MWI), and abundance (A) observed in November in baie de Gaspé. Regressions were based on the model $\log_{10} Y = \log_{10} u + v(\log_{10} X)$ where Y is a predicted value of P, u is the y-axis intercept, v is the slope, and X is the considered index.

Index	P vs. MS	P vs. B	P vs. MWI	P vs. A
R^2	0.9769	0.9704	0.8309	0.2449
Prob > $\|T\|$	0.0978	0.1155	0.2759	0.1623
Intercept (u)	−1.8704	0.2907	6.4820	−21.714
Slope (v)	2.5569	1.4659	1.5632	5.8153
95% confidence limits	7.4881 and −2.3743	4.6713 and −1.7394	9.730 and −6.604	69.249 and −59.144

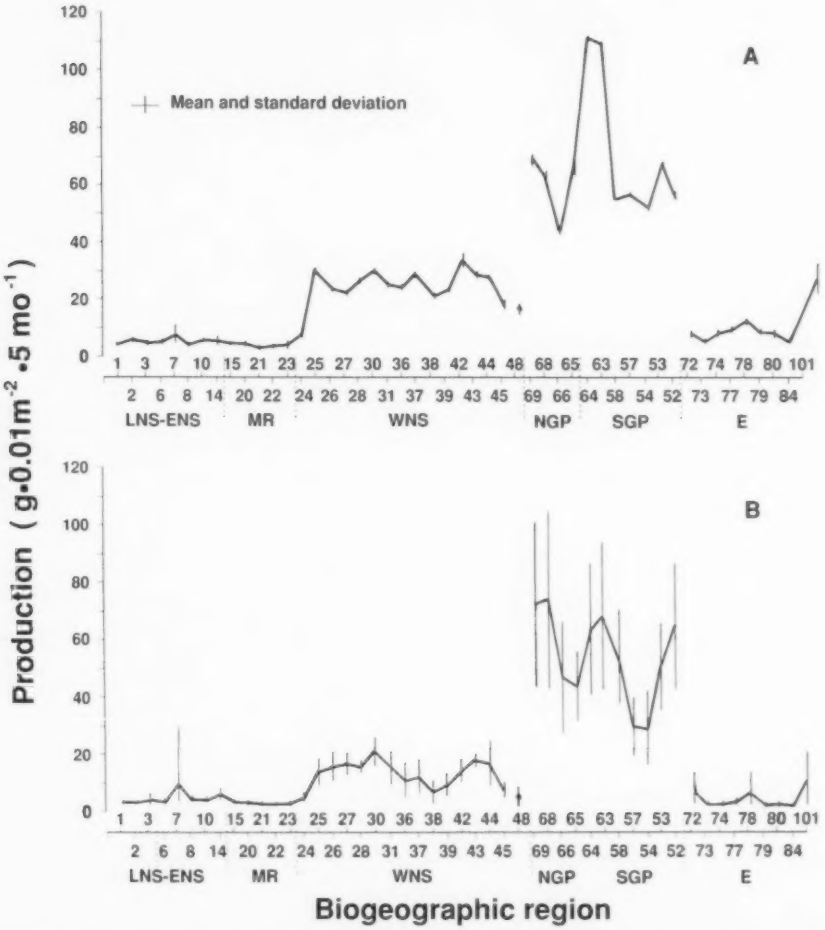

FIG. 4. Mean interannual variation of production estimates (Y) for each of the two best allometric indices of production: (A) maximum size and (B) maximum biomass. Values correspond to collectors moored in the different biogeograhpic regions of the system during the period 1975–85. LNS–ENS, Lower North Shore – Eastern North Shore; MR, Mingan Region; WNS, Western North Shore; NGP, Northern Gaspé Peninsula; SGP, Southern Gaspé Peninsula; E, Estuary.

production in baie de Gaspé (Table 4) find their practical application in estimating production from the mean values of maximum size and maximum biomass observed elsewhere in the system during the period 1975–85. This exercise is based on the assumption that these empirical relationships hold for the other regions of the system and are constant over time, and thus must be considered as yielding only rough approximations of mussel productivity in these areas. Results in Fig. 4 show the Gaspé Peninsula and the western North Shore as potentially the most productive regions and the Estuary, the Mingan, and the

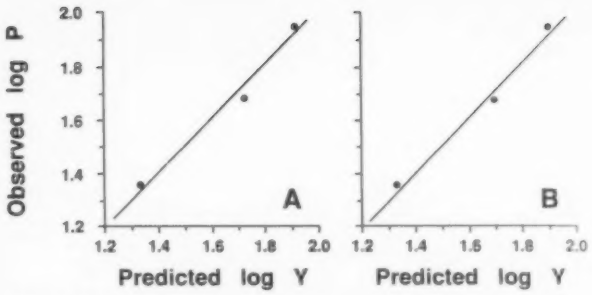

FIG. 5. Relationship between the logarithm of predicted production (log Y) and the logarithm of the observed production (log P) for each of the two best allometric indices of production: (A) maximum size and (B) maximum biomass. The line represents a 1:1 relationship.

eastern North Shore – Lower North Shore regions as potentially the least productive.

Are the above relationships reliable? This question may be partially answered by examining (1) the predictive precision of these equations, (2) the range of values upon which these relationships were established, and (3) the growth conditions during the period of study. The relationship between the predicted production (Y) and the observed production (P) for each of the two variables shows that, for the range of size values considered, production is predicted, respectively, with 97.7 and 99.1% precision (Fig. 5). The range of production, size, and biomass values on which the equations were based is rather limited, since this range included only intermediate and high values (22.9–88.0 g·0.01 m^{-2}·5 mo^{-1}, 18.0–30.2 mm, and 5.2–12.7 g·0.01 m^{-2}, respectively). However, as these values were obtained from the site showing the highest mean abundance and mean growth rate values of *Mytilus* in the system (Fig. 3B and 3C), it can be argued that the upper limit of mussel production likely to be observed in the system is fairly well represented. In contrast, production estimations based on smallest sizes (0–18.0 mm) and biomass (0–5.2 g·0.01 m^{-2}) were not included in the models. Thus, production estimates for these ranges of values have to be obtained by linear extrapolation of the relationships. This point is closely related to the third element of the question. Since growth was roughly continuous from the onset of settlement until the retrieval of buoys (Table 2), a linear extrapolation carried out on a double logarithmic graph may be relevant only if the line has a zero intercept. In both cases (biomass and size equations), the null hypothesis that the regression lines coincided with the origin could not be rejected. Thus, a mussel population of an infinitesimal size or biomass (e.g. 400 μm, the upper size of primary settlers: McGrath et al. 1988, or 0.0001 g·0.01 m^{-2}, respectively) should also be characterized by an infinitesimal production. The result of these operations, 1.29×10^{-3} g·0.01 m^{-2}·5 mo^{-1} (95% confidence limits: 6.41×10^{-3}, 2.6×10^{-4}) and 2.673×10^{-6} g·0.01 m^{-2}·5 mo (95% confidence limits: 0.056, 17.6), satisfy this assumption. Although results in Fig. 4 differ depending on which variable, biomass or maximum size, is used, these values give clear indications of the relative order of magnitude of mussel production among regions.

Limits to Production

At the scale of the mussel patches

In natural populations of mussels, production could be limited by physiological stress (Koehn and Bayne 1989), food availability (Jørgensen 1976; Newell et al. 1989), primary space (Paine and Levin 1981; Navarrete and Castilla 1990), and predation (Dare 1976; Gardner and Thomas 1987). In our study, the suspended position of the collectors maximize food availability and reduces predation and physiological stress considerably. Hence, in mussel patches, the high densities observed suggested that space is the factor most limiting production. The influence of space constraints was therefore closely examined.

In agreement with Eq. (2), in our study the decrease in abundance was accompanied by an increase in weight of mussels (except for size class 1, density 3). However, the trajectory of this relationship varied according to the initial population density and the size class considered (Table 5). The slope fluctuated between -0.33 and -0.98 with corresponding intercept values varying between 1.26 and 2.24, respectively. The relatively low coefficients of determination (0.16–0.63) together with the positive regression coefficient observed for size class 1 (density 3) can be explained, in part, by the high intragroup variability in the samples. On the basis of the 95% confidence limits of v, the theoretical value -0.5 for the self-thinning model could not be rejected in three of six situations. All three situations corresponded to intermediate and high initial population densities.

These results were reached even though the populations studied were immature and settlement was continuous, a phenomenon which could constitute a source of interference for allometric growth of the presettled organisms. Under these conditions, the separation of populations in size classes allowed us to consider organisms of the same age and to reduce sources of errors in the calculations. Indeed, when all organisms (all classes) are used instead of particular size classes, and this for each of the three initial population densities (not shown), the self-thinning model is not verified. This is probably due to the fact that mussels of different size are distributed in many strata and, consequently, the allometric growth in relation to occupation of space is not optimal (Hughes and Griffths 1988; Norberg 1988).

Self-thinning can be interpreted as a measure of the carrying capacity K in models of population dynamics, expressed as a joint function of the number of individuals and their biomass (Westoby 1981, 1984). Consequently, if under conditions of self-thinning, space becomes a limiting factor and the biomass observed by the end of the mooring period at a given site corresponds to maximum values, it is likely that the resulting production estimates in crowded mussel patches also correspond to estimates nearing the maximum values.

At the scale of the system

A shift from fine to coarse spatial scales introduces a further ecological factor affecting production, geographical distance. The importance of this factor is related to the fact that resources are not distributed uniformly or at random, but are structured in space (Fahrig and Merriam 1985; Fahrig and Paloheimo 1988a, 1988b; Nagylaki 1988; Legendre and Fortin 1989). Thus, production can vary considerably from one region to another depending on both the number of successful recruits reaching a given area and the carrying capacity of the environment, which is responsible for growth. In a previous study, Ardisson et al. (1990) showed that, during the period 1975–84, the biomass structure of *M. edulis* in the Estuary–Gulf system was spatially autocorrelated and that the type of spatial structure observed (gradient or patch) depended on the spatial scale at which the system was examined. A better understanding of the

TABLE 5. Temporal changes in the relationship between density and biomass for size classes 1 and 2 for each initial population density from equation $B = CN^{-0.5}$ where B is the biomass, N is the density, C is a constant, and -0.5 is the regression slope.

	Density 1		Density 2		Density 3	
	1	2	1	2	1	2
N	35	33	31	30	36	30
R^2	0.5766	0.6180	0.2786	0.6341	0.0399	0.1581
Prob > |T|	<0.0010	<0.0010	<0.0010	<0.0010	<0.0010	<0.0010
Intercept (C)	1.9276	1.2588	1.7677	1.6873	−1.4296	2.2360
Slope (β)	−0.5497	−0.3323	−0.6034	−0.5245	0.4250	−0.9780
95% confidence limits	−0.6763 and −0.4230	−0.4075 and −0.2570	−0.7981 and −0.4088	−0.6473 and −0.4017	−0.5701 and 0.2798	−1.3253 and −0.6307

processes underlying this structure and its link with production requires more specific studies on larval population dynamics and the patterning effects of the environment itself.

The identification of areas maximizing recruitment, growth, and production of *M. edulis* at the scale of the Estuary–Gulf system has clear implications for the aquaculture of this species. Therefore, these results could have a direct impact on (1) the actual geographical limits of the blue mussel culture and (2) understanding the aquaculture potential of each region, and managing and developing the farming industry in this area.

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A Method for Estimating Gillnet Selectivity of Walleye (*Stizostedion vitreum vitreum*) in Multimesh Multifilament Gill Nets in Lake Erie, and Its Application[1]

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A new method is described for adjusting gillnet catches for gear selectivity. Twelve years (1978–89) of walleye (*Stizostedion vitreum vitreum*) catches (n = 10 761) were pooled to derive frequency distributions of the ratios of fish girth and mesh perimeter for 11 mesh sizes. A gamma function was fitted to each of the 11 frequency distributions so that a selectivity curve could be derived for experimental gill nets used in Lake Erie, or any combination of meshes. An encounter model based on the swimming speed of walleye was used to estimate the probability of walleye encountering gill nets. Adjustments were made to walleye catches for both retention and encounter probabilities. Annual mortality and recruitment rates were compared for standardized and raw data from 1978 to 1989.

Le présent article décrit une nouvelle méthode pour ajuster les prises au filet maillant à la sélectivité des engins de pêche. On a regroupé les données sur les prises de doré (*Stizostedion vitreum vitreum*) (n = 10 761) portant sur une période de 12 ans (1978–1989) dans le but de calculer, pour 11 grandeurs de maille différentes, les distributions de fréquences des rapports entre la circonférence des poissons et le périmètre des mailles. Une fonction gamma a été ajustée à chacune des 11 distributions de fréquences de façon à pouvoir calculer une courbe de sélectivité pour les filets maillants expérimentaux utilisés dans le lac Érié ou pour toute combinaison de mailles. Un modèle de contact poisson-filet reposant sur la vitesse de déplacement du doré a servi à évaluer la probabilité que des dorés entrent en contact avec des filets maillants. Les prises de doréont été ajustées pour obtenir les probabilités de contact avec les filets et de rétention. Les taux annuels de mortalité et de recrutement ont été comparés pour les donnée brutes et normalisées de 1978 à 1989.

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Adjustments in catches of fish for selectivity of gill nets are made primarily to reduce bias and, therefore, to increase accuracy of population parameters. Having removed bias, one then attempts to improve precision by reducing measurement errors. Bias is the magnitude and direction of the consistent deviation of an estimated population parameter from the true one whereas precision is a measure of random errors (Green 1979). Whether one uses samples of harvests or experimental catches, it is necessary to know what part of the population size structure is being sampled. Samples of fish populations are biased if the sampling gear does not catch all size-classes equally well. The difference between the probability of a fish being caught in the sampling gear and the probability of being truly randomly sampled is determined in part by the selectivity of the gear. Gill nets are known to be highly selective (Hamley 1975) and a net of a particular mesh size will retain fish from a restricted size range. However, when gear selectivity has been estimated, sampling bias can be corrected. Assuming that all available habitats are sampled, one can reduce bias by increasing the number of mesh sizes, by restricting the size range used for parameter estimation, or by adjusting the samples for gear selectivity.

Two basic methods have been employed to estimate the selectivity of gill nets. First, a direct measure of selectivity has been made of the proportion of tagged fish of different sizes that were recaptured in gill nets of known mesh sizes (Hamley and Regier 1973; Cucin and Regier 1965). Second, indirect estimates of selectivity have been made by determining the size of fish caught in specific mesh sizes (Baranov 1948; Holt 1963; Van Densen 1987) or by describing the probability function of capture by size in a series of graded-mesh gill nets (McCombie and Fry 1960). In both types of studies, one of the main problems was to find a mathematical description of the selectivity curve. Holt (1963) and McCombie and Fry (1960) assumed that the distribution was approximately normal, but both admitted that a skewed distribution was more appropriate. In contrast, Hamley and Regier (1973) combined separate Pearson type I curves for wedged and tangled walleye (*Stizostedion vitreum vitreum*) to describe a bimodal selectivity curve. The Pearson Type I curve (beta function) has four parameters, and therefore, the bimodal curve of Hamley and Regier (1973) requires the estimation of eight parameters. We have found no evidence that the selectivity curve for walleye in Lake Erie is bimodal and that selectivity may be more adequately described by the

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TABLE 1. Number of sets and walleye samples from Lake Erie (1978–89).

	Gear							
	Western basin				Central basin			
Year	Bottom		Canned		Bottom		Canned	
1978	6[a]	677[b]	1	18	0		0	
1979	6	309	4	104	0		0	
1980	5	99	6	700	0		0	
1981	6	124	6	133	0		0	
1982	6	77	6	230			2	30
1983	6	361	6	488	2	20	2	32
1984	6	565	6	234	1	6	2	42
1985	6	443	6	174	2	127	2	197
1986	5	353	6	145	2	33	2	94
1987	0		8	1133	0		12	1584
1988	0		10	821	0		6	547
1989	4	91	7	218	4	20	15	532
Total		3099		4398		206		3058

[a]Sets.
[b]Total number of walleye = 10 761.

gamma function which requires the estimation of only three parameters. Regier and Robson (1966) described a method for estimating gillnet selectivity for lake whitefish (*Coregonus clupeaformis*), based on the gamma function. Our method differs little, except for our inclusion of the offset value of a. In general, Regier and Robson (1966) had little success in generating the selectivity curve by using the gamma function, unless some restrictive assumptions were employed. We chose the gamma function because first, the frequency distribution was skewed to the right, second, it required only three parameters, and third, the gamma function could provide a description of a retention process that did not differ much over a range of mesh sizes.

In this study, we have used a gamma function (Durand 1971) to describe the frequency distribution of various sized fish caught in different mesh sizes and thereby derive a selectivity curve (retention probabilities) based on the efficiencies of each mesh size. Independent of this, we have adjusted for encounter probability as a function of swimming speed. Although methods for correcting selectivity exist, there is a dearth of applications (McCombie and Fry 1960; Hamley and Regier 1973; Willis et al. 1985). Thus, we have compared trends in recruitment and mortality for uncorrected and standardized catches of walleye from 1987 to 1989 in Lake Erie. This comparison was done to determine if sampling bias was more important than precision in the estimation of catch per unit of effort.

Sampling Methods

Gill nets were set overnight in the Western and Central basins of Lake Erie, using a fixed site sampling design from 1978 to 1986 and then a stratified random design. From 1978 to 1986, a maximum of six fixed locations were sampled in the Western basin of Lake Erie (82 30–83 05′W) in Canadian waters; subsequently, randomly selected locations were added to the shallow- (<10 m) and deepwater strata (>10 m) (Table 1). The western portion of the Central basin (81 30–82 30′W was sampled at two locations from 1982 to 1986 and then at a maximum of 15 randomly stratified stations from 1987 to 1989. The two strata selected in the Central basin were in shallow (<15 m) and deep water (>15 m). Usually, gill nets were set both in the water column (buoyed gill nets were hung on 1- or 3-m strings) and on the bottom at the same locations in both basins, except in 1987 and 1988 when no gill nets were set on the bottom (Table 1). In 1989, a few gill nets were set on the bottom at the same location as the buoyed gill nets.

The multifilament clear nylon gill nets consisted of 11 panels, each measuring 33 m in length (web/line ratio = 1.83–2.16; 210/2 thread). The stretched mesh size and sequence of these 11 panels was as follows: 114, 57, 95, 51, 89, 108, 64, 76, 70, 102 and 83 mm. Forklength (millimetres), round weight (grams), sexual maturity, and age (scales) were recorded for all walleye caught in each panel. We had no information describing how the walleye were caught in the gill nets. Thus, we could not distinguish between tangled, gilled, or only wedged fish. Girth (millimetres) measured just anterior to the first anterior dorsal fin and forklength (millimetres) were obtained from samples of walleye (147 males and 128 females) taken from the Bay of Quinte in Lake Ontario in multigrade multifilament gill nets set from January to October in 1962 (male girth = $0.553L + 1.873$, $r^2 = 0.92$, df = 1,147; female girth = $0.712L - 63.190$, $r^2 = 0.95$, df = 1,128). These girth measurements were adequate for the development of our methods, but more extensive data would be required to investigate annual or seasonal changes in condition.

Development of the Model

Retention Model

Samples from each of the 11 panels (mesh sizes) were pooled across locations and sampling years. The girth of each fish was estimated from its forklength. We use forklength rather than weight because forklengths are more generally available. The ratio of the estimated girth to the circumference of the mesh (girth perimeter (GP) ratio) was calculated for each individual. Each individual was assigned to GP class with a minimum range of 0.02. Each range was incremented in steps of 0.035 unit until at least 10 individuals were assigned to each category, so that the chi-square minimization procedure was not based on small sample sizes, particularly for the larger GP categories at the tails of the distribution.

We then attempted to find the generalized gamma distribution that best represented the frequency distribution of each panel of gill net. The generalized gamma can be written as (Durand 1971)

$$f(x{:}r, m, a) = \{m\,[m\,(x - a)]^{r-1} \cdot e^{-m(x-a)}\} / (r - 1)!$$

where x = GP ratio, r = shape parameter, m = scale parameter, a = offset from 0, $a = 1$ when girth = perimeter of mesh, and $(r - 1)!$ = gamma (r).

For the samples from each mesh size, the parameter a was fixed and the parameters r and m were estimated by minimizing the chi-square deviations between the observed frequency distribution and that expected from the generalized gamma distribution. These were found using the downhill simplex method of Nelder and Mead (1965) as described in Press et al. (1986).

Initial estimates used in the minimization algorithm were estimated from the first two moments of the GP distribution:

$$m = (\text{mean(GP)} - a)/\text{var(GP)}$$
$$r = m\,(\text{mean(GP)} - a).$$

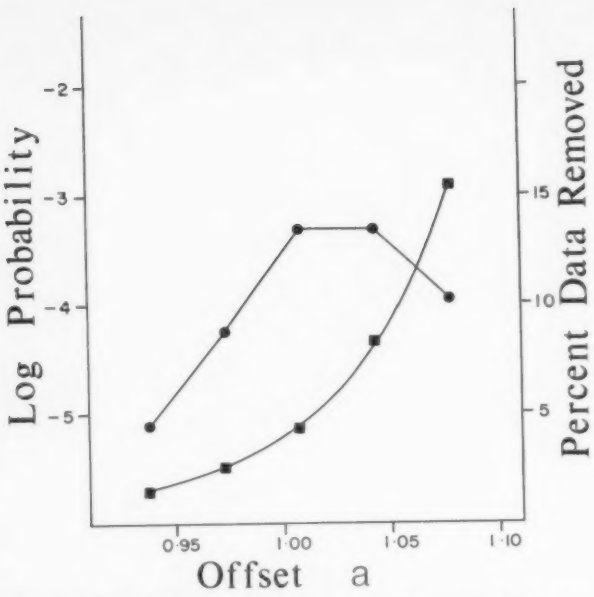

FIG. 1. Log probability (circles) of the observed frequency distribution differing from the gamma distribution and percentage of data removed (squares) from a gamma over a range of offset (a) values for a mesh size of 76 mm.

We were mainly concerned with a description of a process of wedging so that the value of a was about 1. If the walleye's girth was less than the perimeter of the mesh, then it would not be wedged ($a < 1$). However, because of the errors in the estimation of girth, we investigated the effect of variations of a from 0.93 to 1.08 on the estimation of the gamma function. Girths were estimated from a regression of girth on length, with some sampling error. It was apparent that fish with a girth much less than the mesh perimeter were not wedged and represented a small fraction of the total sample. Nevertheless, our objective was to estimate the unbiased frequency distribution from our sample of wedged fish. The choice of the value of the parameter a determined what data would be deleted so that all observations less than a were deleted. Furthermore, a local symmetry was assumed for observations around the offset (a). The number of observations in the first category was adjusted by deleting the same number of observations there as were deleted in the category one step over. For example, suppose category i contains n_i observations. If a is chosen to coincide with the beginning of the range of category $i + 1$, then the adjusted number of observations in the first category (category $i + 1$) of the data subset is $n_{i+1} - n_{i-1}$. For each value of a, the parameters r and m were estimated, as well as the proportion of data deleted and the fit of the model (Fig. 1). However, if the scale and shape parameters are to be comparable across mesh sizes, it is necessary to find a single value of a that can be used for all meshes.

Best estimates of the offset (a) were close to a value of 1 for all but the smallest mesh (mesh 51, $a = 1.08$). Figure 1 shows the relationship between the chi-square probability of the observed fit and the percent data lost, over a range of values of a, for a mesh size of 76 mm. In this example ($n = 1200$), the deviations of the observed data from the gamma distribution are significant but less so as the value of a increases. Generally, the probability of a significant deviation of the observed from the expected (gamma) distribution increases with sample size. Thus, only the size distributions from the largest three meshes, with the smallest sample sizes, were not significantly different from the gamma distribution over a wide range of the parameter a. However, the gamma distribution seemed to be appropriate for all distributions of girth by mesh size (Fig. 2).

Although there was a weak tendency for a to decrease with increasing mesh size, the increased complexity of a retention model in which a was allowed to vary did not seem warranted. We decided to fix a at 0.99. This offset (a) results in reasonable fits over all mesh sizes, with less than 4% of the data removed. Generally, as we increased the value of a, both r and m decreased slightly. By fixing a, more data were omitted from the samples of larger mesh sizes (Fig. 3). The loss of information associated with increasing mesh size may be explained more by the girth–length regression than a change in the wedging process corresponding to an increase in the size of the fish. The sampling error for the regression of girth on length increased with length. This apparent increase in sampling error for larger walleye was explained partly by, first, reduced sample size for larger walleye and, second, changes in the morphology for larger fish. We have used an isometric model of girth as a function of forklength; however, it may be possible that the relation between girth and forklength is allometric. Thus, the loss of information with increasing mesh size was probably a function of errors from the estimate of girth from forklength.

There are a number of features of this retention model worth noting. Different meshes show a great deal of similarity in their retention curves. The model GP value of the distributions for the first three small mesh sizes (51–64 mm) was slightly greater than that of the larger mesh sizes which remained constant near 1 (Fig. 2). Smaller walleye may have softer bodies and therefore can be wedged over a greater proportion of their body length. The shapes of the retention curves are similar for all but the two smallest meshes. This change was reflected by changes in the shape parameter (r). The range of GP ratios was reduced as the size of the mesh increased (Fig. 3). Thus, changes in the scale parameter (m) were linearly related to mesh size.

Once the gamma distribution was fitted for each mesh size (Fig. 2), we estimated the efficiency (e_{ij}) of each mesh size (i) for each interval of girth (j) (Table 2). We assumed that all girth intervals were equally available within each mesh size. If the proportion of a size-class captured in a specific mesh size was only dependent on how well the size-class fitted the net, then the efficiencies (e_{ij}) were calculated by integrating over the specified intervals of girth for each mesh size. Thus, we derived a matrix of relative efficiencies by girth interval for each mesh size.

If the total efficiency of a panel is independent of mesh size, then the total area under the curve is equal for all meshes. The relative selectivity coefficient of the gear for each girth interval was calculated first by summing the relative efficiencies of each girth interval across all the mesh sizes in the gear (e_{+j}); then, each total efficiency (e_{+j}) was divided by the maximum total efficiency (E_{+j}) corresponding to the girth interval most likely to be caught in the gear. Thus, from the efficiency of each panel of a specific mesh size, we determined the efficiency of the gear or the specific collection of panels used in Lake Erie.

Encounter Model

If the process determining the way that fish are caught in gill nets is independent of the size of the fish or mesh, then the

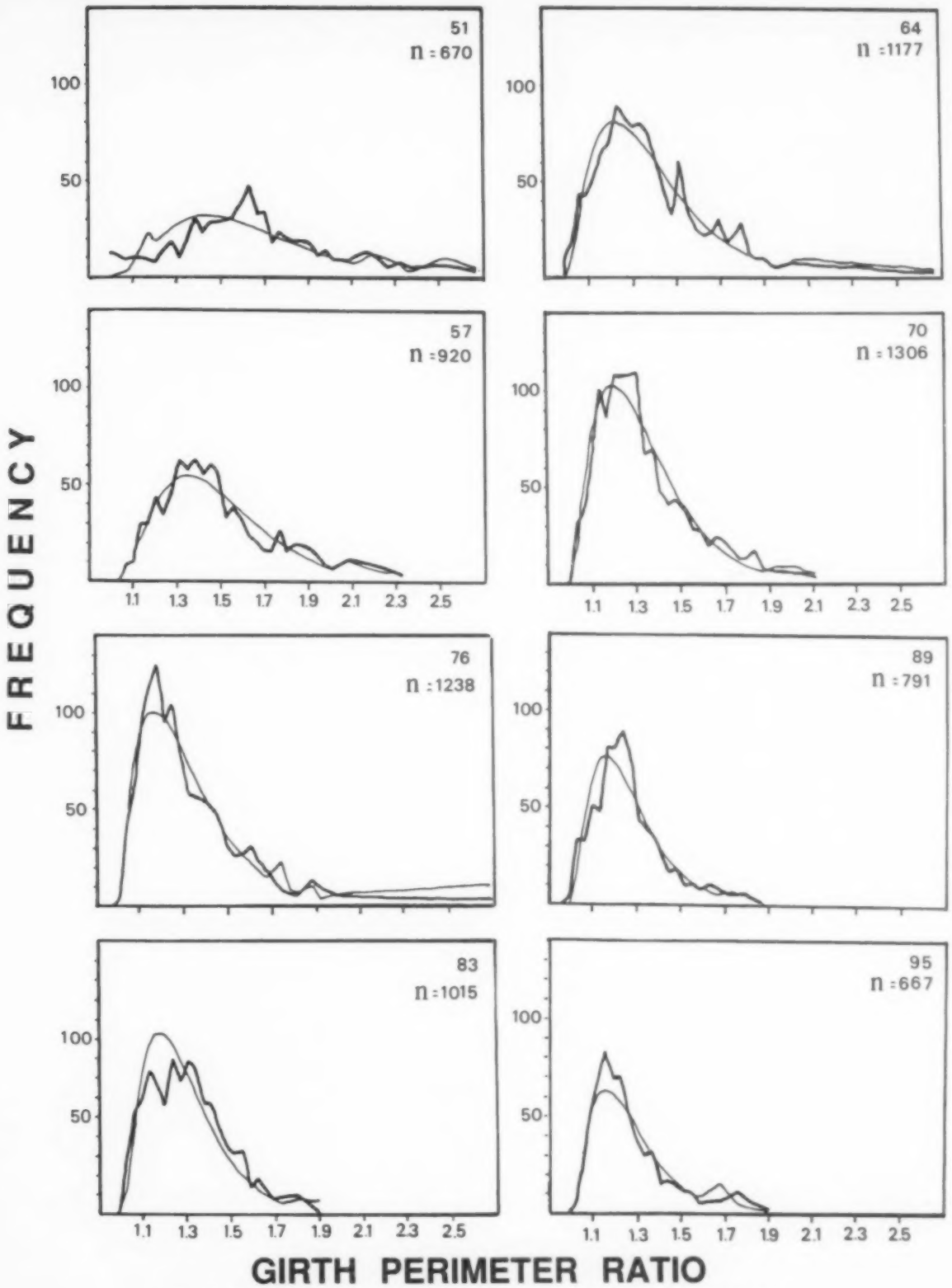

FIG. 2. Observed and gamma distribution of walleye caught in eight different mesh sizes.

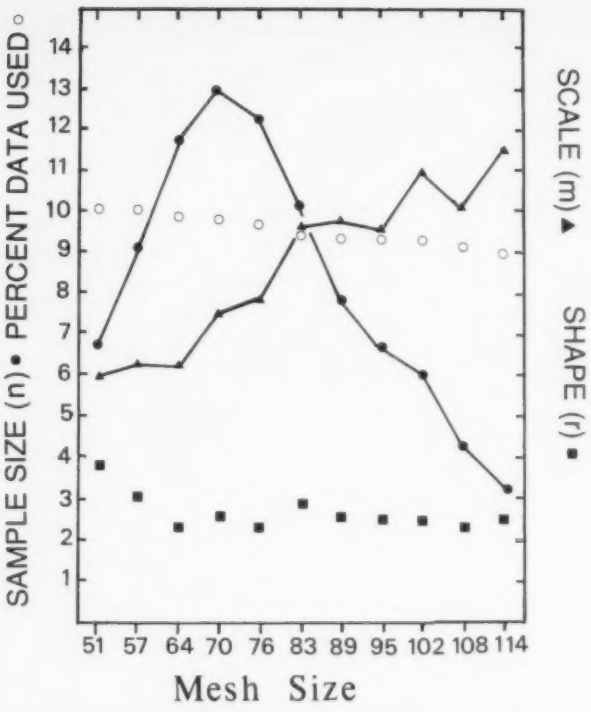

FIG. 3. Shape (r = squares), scale (m = triangles), sample size (n = solid circles; values in units of 100), and percent data remaining (open circles; value in units of 10) over the range of mesh sizes, with an offset (a) of 0.99.

standardized catch should represent an unbiased sample of the population. In practice, this is known not to be the case (Hamley 1975; Rudstam et al. 1984). It seems reasonable to treat the standardized catch as dependent on retention but conditional on gear encounter, hence separating retention from encounter probability. Site- or time-specific models of encounter can then be developed separately.

This model is based on the assumption that the probability of encountering the net increases with swimming speed, a function of body length:

$$R = a L^z$$

where R = probability of encounter and a = constant determined by solving for a with a forklength of 600 mm and $z = 0.5$ (Jones et al. 1974), when $R = 1$. The inverse of the probability of encounter (R) was multiplied by the catch of each forklength interval, after making the correction for selectivity. Applying corrections for both gear selectivity and encounter probability to estimates of catch per unit of effort (CPUE), we estimated annual mortality as the average rate of change of relative abundance (CPUE) for ages 2, 3, 4, and 5 yr from one year to the next ($\log_e (C_{t+1} - C_t)$ where C_t = CPUE by age-class).

Test of the Model

The shape of the relative selectivity curve for our multigrade gill nets was skewed to the right with a peak selectivity coefficient at a girth of 220 mm (Fig. 4). The integrals used to estimate the efficiency of each mesh size for a range of girths (120–390 mm) (Table 2) were based on the fit of the gamma to each mesh size (Fig. 2). The gamma fit for the larger GP categories was more variable because the sample sizes were smaller in these larger categories.

Relative selectivity coefficients (Table 2) were used to calculate standardized frequencies from observed catches. All fish with GP ratios less than a were first deleted from the observed catch. Using this matrix of efficiencies (Table 2), it was possible to calculate the standardized frequencies by girth interval. Standardized frequencies were calculated by dividing the actual catch for each girth interval by the relative selectivity coefficient. The effect of this correction to the number of fish in each girth (length) interval was to increase the abundance of the smallest and largest walleye (Fig. 5). thus, walleye that are not captured well because of their poor fit to the gill net are given a greater weighting.

The matrix of efficiencies can be used to calculate the relative selectivity curve for any combination of meshes. It is then possible to compare the standardized frequencies calculated from samples of all meshes with that derived from any subset of the data (with various combinations of panels (mesh sizes) removed). If a panel was removed, its efficiency was not included in the sum used to estimate relative selectivity. As a result, we found that the standardized frequencies by girth were similar, regardless of the number or type of meshes (panels) removed (Table 3). Thus, we found that the same result could be obtained by using fewer mesh sizes in each gang of gill nets.

Estimates of annual mortality from ages 2 to 6 did not differ markedly between standardized and raw data (Fig. 6). Total annual mortality was more variable in the Central basin, probably because sampling effort was smaller and inadequately stratified. Only since 1987 was the sampling effort in the Central basin increased and stratified. The variability of the estimated mortality rate in 1989 was less than in previous years, possibly because this was the first year when the estimate was based on two consecutive years of more intense stratified sampling. The same phenomenon was not evident in the Western basin, probably because the sampling fraction was larger in the Western than in the Central basin, except in recent years (1987–89). Estimates of standardized mortality rates by age tended to be lower, particularly in the sample from the Western basin where sampling was more intense (Table 4). In the Western basin samples, there was a trend for annual mortality to decline with age (Table 4) for both standardized and raw data.

Although the standardized estimate of numbers at age 1 was higher than the estimate from the raw data, the annual trends were closely related (Fig. 7). In the Western basin (buoyed gill nets: 1978–89), strong year-classes were evident in 1977, 1982, and 1986. Strong year-classes were found in 1982, 1984, and 1986 in the Central basin (1982–89). It is clear that the bias caused by the selectivity of the gill nets is less important than the sampling error in the estimation of CPUE and total mortality rate.

Discussion

The criteria for evaluating estimates of mortality rate and abundance are precision (sampling error) and accuracy (bias). In this study, we have described a method for assessing a systematic component of bias associated with the retention characteristics of multimesh gill nets. One important component of bias that we were not able to assess was the influences of tem-

TABLE 2. Relative efficiencies of different mesh sizes for walleye of different girth measurement and the relative efficiency and selectivity of the gang by girth.

Girth (mm)	Mesh size (mm)											Relative efficiency	Relative selectivity
	51	57	64	70	76	83	89	95	102	18	114		
110	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
120	0.0119	0.0061	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0180	0.0214
130	0.0603	0.0521	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1123	0.1330
140	0.1064	0.1086	0.0384	0.0008	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2541	0.3009
150	0.1303	0.1413	0.1259	0.0667	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.4642	0.5497
160	0.1333	0.1466	0.1571	0.1404	0.0426	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.6203	0.7345
170	0.1224	0.1334	0.1520	0.1607	0.1318	0.0283	0.0000	0.0000	0.0000	0.0000	0.0000	0.7286	0.8627
180	0.1047	0.1112	0.1309	0.1497	0.1587	0.0881	0.0041	0.0000	0.0000	0.0000	0.0000	0.7474	0.8850
190	0.0851	0.0873	0.1054	0.1257	0.1507	0.1294	0.0692	0.0000	0.0000	0.0000	0.0000	0.7527	0.8913
200	0.0666	0.0654	0.0812	0.0991	0.1284	0.1426	0.1320	0.0557	0.0130	0.0002	0.0000	0.7842	0.9286
210	0.0506	0.0473	0.0607	0.0750	0.1028	0.1353	0.1528	0.1424	0.0546	0.0160	0.0001	0.8376	0.9919
220	0.0375	0.0333	0.0443	0.0550	0.0791	0.1171	0.1456	0.1584	0.1011	0.0597	0.0135	0.8445	1.0000
230	0.0273	0.0229	0.0318	0.0395	0.0591	0.0952	0.1249	0.1451	0.1307	0.1020	0.0542	0.8328	0.9862
240	0.0196	0.0155	0.0225	0.0278	0.0433	0.0740	0.1004	0.1217	0.1386	0.1263	0.0953	0.7849	0.9295
250	0.0138	0.0103	0.0157	0.0193	0.0312	0.0556	0.0771	0.0971	0.1297	0.1312	0.1201	0.7012	0.8303
260	0.0096	0.0067	0.0109	0.0133	0.0222	0.0407	0.0574	0.0749	0.1112	0.1223	0.1271	0.5963	0.7061
270	0.0067	0.0044	0.0075	0.0090	0.0156	0.0292	0.0417	0.0564	0.0895	0.1058	0.1205	0.4862	0.5758
280	0.0046	0.0028	0.0051	0.0061	0.0109	0.0205	0.0297	0.0418	0.0687	0.0866	0.1061	0.3829	0.4534
290	0.0031	0.0018	0.0035	0.0041	0.0075	0.0142	0.0208	0.0306	0.0507	0.0681	0.0886	0.2930	0.3470
300	0.0021	0.0011	0.0023	0.0027	0.0052	0.0097	0.0144	0.0221	0.0363	0.0518	0.0710	0.2189	0.2593
310	0.0014	0.0007	0.0016	0.0018	0.0035	0.0066	0.0099	0.0159	0.0254	0.0384	0.0552	0.1604	0.1899
320	0.0009	0.0004	0.0011	0.0012	0.0024	0.0044	0.0067	0.0113	0.0173	0.0279	0.0418	0.1155	0.1368
330	0.0006	0.0003	0.0007	0.0008	0.0016	0.0030	0.0045	0.0080	0.0116	0.0199	0.0310	0.0820	0.0971
340	0.0004	0.0002	0.0005	0.0005	0.0011	0.0020	0.0030	0.0056	0.0077	0.0140	0.0226	0.0575	0.0681
350	0.0003	0.0001	0.0003	0.0003	0.0007	0.0013	0.0020	0.0040	0.0050	0.0097	0.0162	0.0399	0.0472
360	0.0002	0.0001	0.0002	0.0002	0.0005	0.0008	0.0013	0.0028	0.0032	0.0066	0.0115	0.0274	0.0325
370	0.0001	0.0000	0.0001	0.0001	0.0003	0.0005	0.0009	0.0019	0.0021	0.0045	0.0080	0.0187	0.0222
380	0.0001	0.0000	0.0001	0.0001	0.0002	0.0004	0.0006	0.0013	0.0013	0.0030	0.0056	0.0127	0.0150
390	0.0000	0.0000	0.0001	0.0001	0.0001	0.0002	0.0004	0.0009	0.0008	0.0020	0.0038	0.0085	0.0101

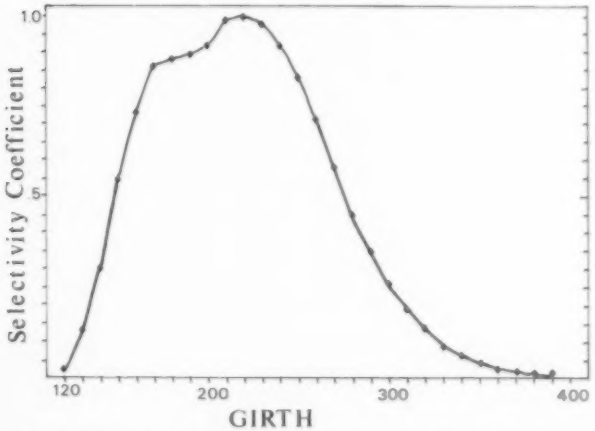

FIG. 4. Selectivity coefficient by girth of walleye for a gill net containing all 11 mesh sizes.

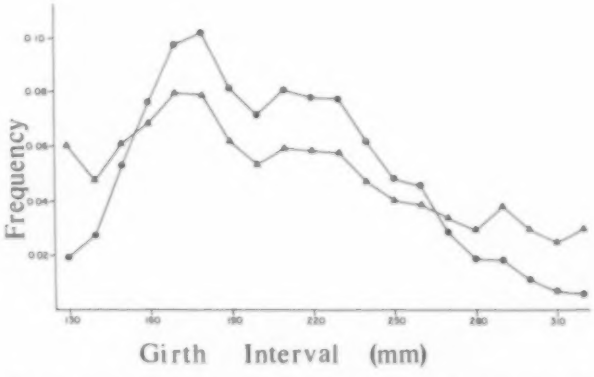

FIG. 5. Observed (circles) and standardized frequencies (triangles) of all walleye captured in the 11 meshes from 1978 to 1989.

poral, spatial, and behavioural stratification of fish by age and size.

Our model of gear selectivity is an indirect method that fits an assumed probability distribution to empirical data. We assume that the principal mechanism for capture is that fish are wedged, to varying degrees, in the gill net. We further assume that the physical mechanisms involved in capture are independent of the size of the fish and mesh, or that the components of the process that depend on size vary systematically (Fig. 3). Obviously, this mode of capture can be complicated by fish tangling their teeth and spines in the filament. Hamley and Regier (1973) distinguished between these two processes of wedging and tangling. We suggest that over most of the size range retained by a net, the two processes are not independent. If a large fish encounters a small-mesh gill net, the probability of it being retained will be a function of both wedging and tangling. From our data we had no way to distinguish between tangled and wedged walleye. Most tangling is preceded by some degree of wedging. In practice, it is difficult to distinguish

TABLE 3. Estimated proportions of sample by girth interval with three different combinations of five mesh sizes removed (Null = full gang; A = 51, 64, 76, 89, and 102 removed; B = 57, 70, 83, 95, and 108 removed; C = 64, 76, 89, 102, and 114 removed). n = 8743; parameter used, a = 0.99; x = A + B + C/3.

Girth (mm)	Null	A	B	C	$\bar{x}$	$\bar{x}$ (NULL)
130	0.060	0.072	0.056	0.057	0.062	+0.002
140	0.047	0.059	0.042	0.041	0.047	0
150	0.061	0.068	0.058	0.059	0.062	+0.001
160	0.069	0.072	0.069	0.065	0.069	0
170	0.080	0.083	0.080	0.080	0.081	+0.001
180	0.079	0.077	0.083	0.072	0.077	−0.002
190	0.061	0.060	0.064	0.060	0.061	0
200	0.054	0.050	0.059	0.049	0.053	−0.001
210	0.050	0.062	0.059	0.062	0.061	+0.001
220	0.058	0.063	0.057	0.062	0.061	+0.003
230	0.057	0.057	0.059	0.058	0.058	+0.001
240	0.047	0.044	0.048	0.048	0.047	0
250	0.0400	0.035	0.039	0.044	0.040	0
260	0.039	0.030	0.036	0.046	0.037	−0.002
270	0.034	0.027	0.033	0.039	0.033	−0.001
280	0.030	0.033	0.029	0.033	0.032	+0.002
290	0.038	0.025	0.038	0.043	0.035	−0.003
300	0.030	0.020	0.030	0.031	0.027	−0.003
310	0.026	0.019	0.029	0.021	0.023	−0.003
320	0.031	0.026	0.033	0.029	0.029	−0.002

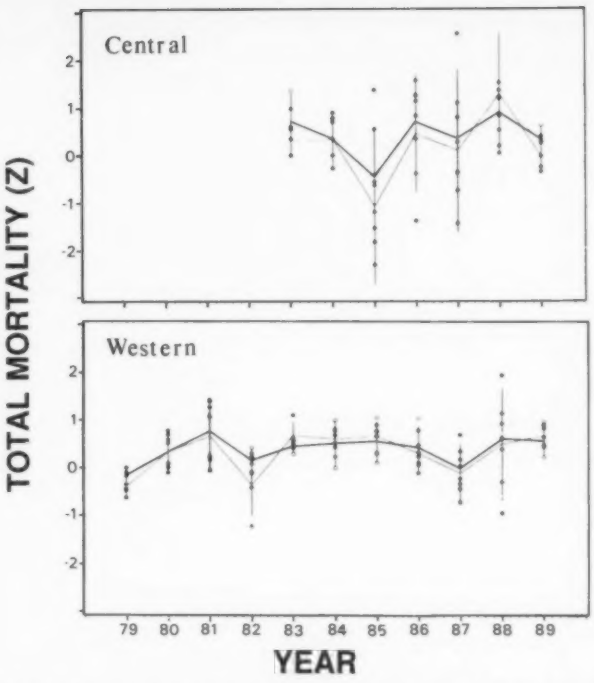

FIG. 6. Average annual instantaneous mortality rates for raw (open circles) and standardized data (solid circles) in the Central and Western basins of Lake Erie.

between wedged and tangled fish. We suggest that the sample size available to Hamley and Regier (1973) for estimating the bimodal curves of wedging and tangling was inadequate. There was no strong indication of a bimodal frequency distribution of length-classes (table 1 of Hamley and Regier 1973). If a bimodal distribution were generally applicable to gillnet selectivity in walleye, it should have been apparent in some range of mesh sizes in our data. We have no evidence for a bimodal frequency distribution by GP ratio for walleye from Lake Erie (Fig. 2).

The systematic changes in the parameter estimates used to model the frequency distributions of GP ratios by mesh size were evident (Fig. 3) because numbers per size class have changed smoothly with size, probably because we combined 11 yr of data. The small reduction in the shape parameter (r) in the first two mesh sizes corresponds to a reduction in the modal GP value for each mesh size. This reduction may have more to do with the way we estimated girth from length than any change in the way fish were caught. The data used for estimating the regression coefficients of girth on length did not encompass the entire range of forklengths used to estimate the gamma. If the relation between girth and length is curvilinear (allometric rather than isometric), then we would underestimate girths for small walleye. Consequently, it would appear that the small fish were caught at higher GP, with a corresponding higher r parameter. The scale parameter m increases linearly with mesh size, and this implies that the relative range of forklengths decreases as mesh size increases. This phenomenon could be explained by, first, as forklength increases, the ability to escape after wedging increases and therefore only the most tightly wedged walleye remain in the net and, second, the absolute range of forklengths is reduced with increasing mesh size because of attrition by mortality. The retention curves rise sharply above a GP ratio of 1 (a = 1) and then drop off in a statistically repeatable manner for each mesh size. When the GP rato equals 1 or greater, a fish cannot easily pass through the mesh. Below this point (excluding errors in the estimate of girth from length), a fish cannot be properly wedged, just tangled. Therefore, only catches of fish that have a GP ratio greater than or equal to 1 can be corrected for gear selectivity by our model. We have chosen not to use fish much below this transition (a) point in our estimates of population parameters. Accurate estimates of population parameters demand either an unbiased sample of the population or a method for correcting the bias. To obtain precise parameter estimates, one must show that the systematic error is relatively larger than the random component. Distribution of individuals in the truncated data sets (a >1) are consistent with a strong systematic process of selectivity.

Although the standardized frequencies show a linearly decreasing trend over most of the range of retained sizes, they still cannot account for the steep drop in the number of smaller fish retained. Therefore, either the retention characteristics of the gill nets change drastically below some size, or the smaller fish are not in the portion of the water column sampled. Small fish may frequent shallow water not sampled by gill nets or may move about so tentatively that they would never be wedged or tangled in nets; thus, there may be size-dependent catchability. The changes in the estimates of the shape parameter for the smaller two meshes may be indicative of a size-dependent transition point in the retention process. If this is the case, then simply adding smaller panels to the multigrade gill nets may not be the most efficient method for obtaining accurate estimates of these smaller fishes.

One further correction that we made explicitly, rather than implicitly (Hamley and Regier 1973), was the adjustment for encounter probability. We assumed that encounter probability was proportional to size-dependent swimming speed. Habitat

TABLE 4. Annual instantaneous mortality rates (± SD) of Lake Erie walleye by age-class. N = number years; raw = uncorrected; Stand = standardized.

	Age (yr)			
	2	3	4	5
		Central		
Bottom				
Raw	0.04 ± 0.528	−0.46 ± 1.042		0.13 ± 0.166
Stand	0.11 ± 0.763	−0.54 ± 1.370		0.38 ± 0.751
n	4	4		4
Canned				
Raw	−0.40 ± 0.819	−0.42 ± 0.856	−0.44 ± 0.550	−0.39 ± 0.703
Stand	−0.11 ± 0.912	0.04 ± 1.222	−0.58 ± 1.405	−0.55 ± 1.811
n	7	7	7	7
		Western basin		
Bottom				
Raw	−0.42 ± 0.559	−0.33 ± 0.393	−0.08 ± 0.255	−0.07 ± 0.154
Stand	−0.31 ± 0.638	−0.28 ± 0.467	−0.10 ± 0.372	−0.17 ± 0.502
n	9	9	9	9
Canned				
Raw	−0.66 ± 0.468	−0.53 ± 0.511	−0.15 ± 0.277	−0.21 ± 0.339
Stand	−0.46 ± 0.456	−0.40 ± 0.594	−0.09 ± 0.646	−0.38 ± 0.785
n	11	11	11	11

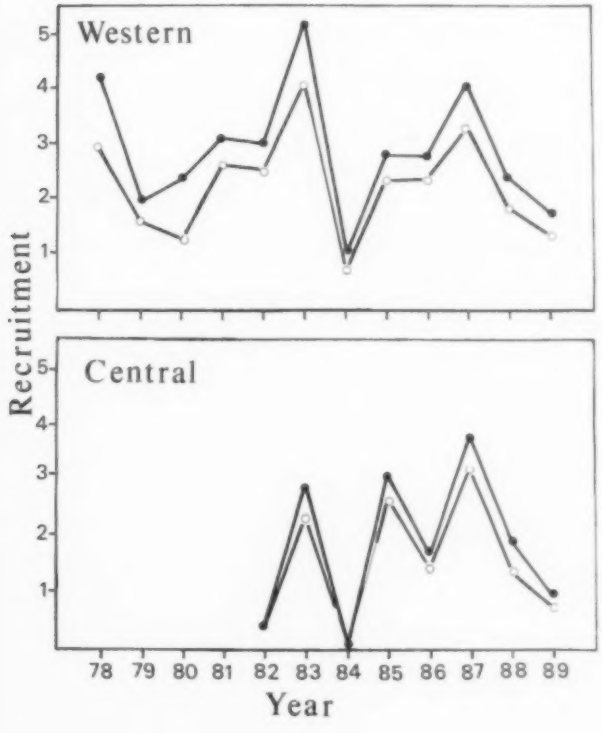

FIG. 7. Annual recuitment (catch per gang of multimesh gill nets) of 1-yr-old walleye in October, using raw (open circles) and standardized data (solid circles).

use, time spent feeding, and ontogenetic changes in behaviour could also affect encounter speed (McConville and Fossum 1981). With adjustments for retention and encounter probabilities, the efficiency of 114-mm gill net was only twice that of 51-mm mesh whereas the differential in Hamley and Regier (1973) was aproximately 20-fold. Obviously, swimming speed cannot explain the 20-fold difference in efficiency estimated by Hamley and Regier (1973). One would not expect that size-dependent survival from tagging could explain this differential in efficiency. However, if larger walleye spent a larger portion of their time searching for prey, then the probability of encountering would increase. Thus, encounter probability could be a function of the availability of suitable prey (Holling 1966). Further adjustments could be made to the selectivity model to account for the attritions of size-classes by mortality. Estimating the components of the efficiency matrix (Table 2), we have assumed that equal numbers of fish are available for capture in each size-class and mesh size. However, one could estimate the relative abundance by size-class if one knew what the mortality rate was by size- and age-class within and among meshes. The selectivity model is dependent on the ratio of fish girth and mesh perimeter, and therefore, the model explains the selectivity of the gear for a larger range of girths as the mesh size increases (Fig. 2). Thus, the decrease (mortality) in the number of fish available to a mesh increases with increasingly larger mesh sizes. This may explain why the scale parameter (m) increases with mesh size, implying that the distribution of GP ratios is more skewed in larger mesh sizes (Fig. 3).

Our corrections for encounter are done separately from the selectivity. It may be possible to use mortality rates to estimate encounter probabilities, independent of swimming speed. The frequency distributions could be generated by applying a mortality rate related to age- and size-classes. Then one could calculate what encounter model would transform the standardized frequencies (from the gamma) to the frequencies expected from the mortality model.

Conclusions

A method that allows one to adjust for selectivity by treating retention and encounter probabilities separately may be more generally useful (Rudstam et al. 1984) than one that incorporates both factors in estimates of the parameters of the selectivity curve (Hamley and Regier 1973). Our method that determines retention probability may be similar between years, lakes, and seasons, if one allows for changes in the relation between girth and forklength. Encounter probability may account for much of the variation between lakes, seasons, and years and may be largely a function of size-selective prey availability. Therefore, without further information about the effect of variations in prey density, an application of our selectivity function to other walleye populations would provide a standardized correction, but not necessarily a true correction, of the size composition of the population.

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Potential Rates of Increase of a Harbour Porpoise (*Phocoena phocoena*) Population Subjected to Incidental Mortality in Commercial Fisheries

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Woodley, T. H., and A. J. Read. 1991. Potential rates of increase of a harbour porpoise (*Phocoena phocoena*) population subjected to incidental mortality in commercial fisheries. Can. J. Fish. Aquat. Sci. 48: 2429–2435.

We estimated the potential intrinsic rate of increase (r) of the harbour porpoise (*Phocoena phocoena*) population in the Bay of Fundy and Gulf of Maine using empirical data on reproductive rates (m_x) and several hypothetical survival (l_x) schedules. Schedules of l_x to maximum ages of 12 and 15 yr, were calculated from two potential natural mortality (n_x) schedules combined with several schedules of incidental mortality (h_x) estimates. The most realistic results were obtained when n_x of non-calves were calculated from Caugley's (1966. Ecology 47: 906–918) smoothed age-frequency equation for Himalayan thar (*Hemitragus jemlahicus*) and applied in conjunction with a range of calf natural mortality estimates. This model indicates that harbour porpoises have a limited capacity for population increase, and populations are unlikely to sustain even moderate levels of incidental mortality (4% of the population per year). Extending the maximum age used in the models from 12 to 15 yr does little to increase estimates of r for the harbour porpoise population, and hence their susceptibility to incidental mortality.

Nous avons estimé le taux intrinsèque potentiel d'augmentation (r) de la population de marsouin commun (*Phocoena phocoena*) dans la baie de Fundy et le golfe du Maine à l'aide de données empiriques sur les taux de reproduction (m_x) et de plusieurs tableaux de survie (l_x). Les tableaux de survie jusqu'à des âges de 12 et 15 ans ont été calculés à partir de deux tableaux de mortalité naturelle possible (n_x) combinés à plusieurs tableaux d'estimations de mortalité accidentelle (h_x). Les résultats les plus réalistes ont été obtenus lorsque n_x non-petits ont été calculés à partir de l'équation de Caugley (1966. Ecology 47: 906–918) pour la fréquence lissée des âges de *Hemitragus jemlahicus* et appliqués de concert avec une gamme d'estimations de la mortalité naturelle des petits. Ce modèle indique que le marsouin commun a une capacité limitée de se multiplier et qu'il est peu probable que les populations maintiennent des niveaux même modérés de mortalité accidentelle (4 % de la population par an). Porter la limite d'âge des modèles de 12 à 15 ans fait peu augmenter les estimations du taux r de la population de marsouin commun, et donc leur susceptibilité à une mortalité accidentelle.

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Harbour porpoises (*Phocoena phocoena*) in Canadian waters have been accorded "threatened" status by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), largely in response to the effects of incidental mortalities in fishing gear (Gaskin 1989). Harbour porpoises in the Bay of Fundy and Gulf of Maine appear to form a discrete population unit (Gaskin 1984) and are subjected to considerable mortality in commercial fisheries (Read and Gaskin 1988). The majority are killed through incidental catches in groundfish gill nets, although a small number of individuals are also entrapped and killed in herring weirs (Read and Gaskin 1988; Polacheck 1989). Concern has been expressed over the impact of these catches because preliminary data indicate that the level of incidental mortality may be large relative to population size (Read and Gaskin 1988). Decreases in relative abundance in the late 1970s were noted in some areas in the Bay of Fundy (Gaskin and Watson 1985), and anecdotal evidence suggests that such decreases continue today (D. Gaskin, pers. comm.). Little is definitively known, however, about the resilience of this harbour porpoise population to such incidental mortality.

Demographic models can be used to evaluate the effects of the removal of animals from a population and are particularly useful in understanding the constraints on population growth imposed by life history parameters (Barlow 1989). In preliminary analyses, Barlow (1986) and Barlow and Boveng (1991) have used demographic models to demonstrate that phocoenids have limited potential for population growth, although these studies have been hampered by a lack of age-specific data on reproduction and survival.

In this paper we present models for evaluating the potential intrinsic rate of increase (r) of the harbour porpoise population in the Bay of Fundy and Gulf of Maine. We use reproductive rates derived from Read (1990a), two potential schedules of natural mortality, and several estimates of the proportion of the population subjected to incidental mortality. Age-specific mortality is not known, but reasonable approximations are inferred from knowledge of maximal ages (Barlow 1986, 1987). Although it is not known whether current estimates of abun-

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dance and incidental catches of this harbour porpoise population are accurate, we use existing data to estimate likely upper and lower bounds of these parameters.

Methods

Equation Formulations

Estimates of intrinsic rates of increase (r) of harbour porpoise were calculated by solving a summation equivalent of Lotka's characteristic integral equation (e.g. Lotka 1939) using constant age-specific schedules of natural mortality and reproductive rates. Because there has been considerable discussion regarding appropriate formulations of discrete versions of Lotka's equation (Goodman 1982; Caswell 1989), we will be explicit in the formulation used here.

Harbour porpoises from the Bay of Fundy and Gulf of Maine are annual breeders with parturition mainly concentrated in May (Read 1990b). Hence they are representative of a "birth-pulse" population (Caughley 1977). A summation sign can be substituted for the integral sign in Lotka's equation for such populations (Cole 1954; Eberhardt 1985), giving

$$(1) \quad 1 = \sum_{x=a}^{w} e^{-rx} l_x m_x$$

where survival (l_x) is the probability of an individual surviving the interval from birth to age x (thus, $l_0 = 1.0$), age-specific reproductive rate (m_x) is the number of offspring produced by an individual aged x at the birth-pulse beginning the next 1-yr interval, w is some maximal age, and a is the age of first reproduction. (While l_x is most realistically regarded as continuously changing in time, the product $l_x m_x$ in equation (1) is typically discontinuous because m_x is discontinuous (Cole 1954).) Following the convention for sexually reproducing species, both l_x and m_x are expressed in terms of females only; l_x represents survival of females and m_x represents female offspring per female. Values of r were derived using an iterative algorithm programmed in FORTRAN.

With constant l_x and m_x schedules, a "stable" age distribution will eventually be achieved by a population growing at the rate r. The age structure of the population can then be described in terms of the proportions of each age class (c_x) over the age interval x to $x + 1$, by combining equations (5) and (18) from Cole (1954), as

$$(2) \quad c_x = e^{-rx} l_x \Big/ \left[\sum_{i=0}^{w} e^{-ri} l_i \right].$$

To provide an indication of the suitability of our models, c_w were calculated and compared with empirical data from the Bay of Fundy and Gulf of Maine harbour porpoise population.

Age-Specific Reproductive Rates

Pregnancy rates can be utilized for m_x data (Eberhardt 1985). Based on the presence of a corpus luteum, Read (1990a) established the proportion of pregnant females in each age class (numbering the first age class 0) of harbour porpoises from a sample of 108 caught incidentally in gill nets in the Bay of Fundy between July and Sepember 1985–88. Using these proportions and assuming that all females pregnant in age class x give birth at their next birthday (age $x + 1$), and a male to female sex ratio of 1:1 at birth, produces the estimates of age-specific m_x rates used in the models (Table 1). This m_x schedule represents a maximum for the population because it does not account for infertility resulting from unsuccessful implantation, abortion, or foetal resorption. We used pregnancy rates based on the presence of a corpus luteum rather than foetuses because harbour porpoises ovulate and conceive in late June, but foetuses are not detectable until early August (Read 1990b).

TABLE 1. Age-specific reproductive rates and proportions of female harbour porpoises from a sample of 108 killed in gill nets in the Bay of Fundy during 1985–88 (Read 1990a) and age proportions calculated from the smoothed age-frequencies of Himalayan thar from Caughley (1966).

Age (x)	Reproductive rate (m_x)	Age proportions (c_x)	
		Porpoises	Thar
0	0.0	0.08	0.25
1	0.0	0.18	0.12
2	0.0	0.20	0.12
3	0.10	0.20	0.11
4	0.36	0.11	0.10
5	0.50	0.10	0.08
6	0.50	0.06	0.07
7	0.50	0.04	0.05
8	0.50	0.00	0.04
9	0.50	0.00	0.03
10	0.50	0.01	0.02
11	0.50	0.00	0.01
12+	0.50	0.01	0.01

Age-Specific Survival

Age-specific l_x were calculated from survival rates (p_x) of age classes (the proportion of animals alive at age x that survive to $x + 1$) where $l_{x+1} = p_x l_x$ (Caughley 1977). Maximum ages w were established in the models by setting $p_w = 0$, i.e. all individuals which survive to age w die before reaching $w + 1$. Like Barlow (1986), we used a w of 15 yr for harbour porpoises in the models. In the sample of 108 females from Read (1990a), however, only a single individual exceeded 12 yr of age (Table 1) and no individuals were of age 15 or more, so we also used a maximum age of 12 yr.

Survival rates can be partitioned into isolated rates of natural mortality, n_x (the proportion of age class x that would die from natural causes if there were no hunting), and hunting mortality, or in our case incidental mortality, h_x (the proportion of age class x that would die incidentally in fishing gear if no animals died from natural causes), by the formula

$$(3) \quad p_x = (1 - h_x)(1 - n_x).$$

With this formula there is no need to assume that rates of incidental and natural mortality are proportional throughout the year (Caughley 1977). Several schedules of n_x and h_x values were used in our models.

Natural mortality rates

We used two methods of representing n_x in the models to explore the potential r for this population. In the first, hereafter referred to as model A, we followed Barlow (1986) and assumed a single p_x for non-calves over all age classes >0 varying from 0.71 t 0.90; in the absence of incidental mortality, this is equivalent to n_x ranging from 0.29 to 0.10, respectively. Calves (age class 0) are probably dependent on their mothers for their first year of life (Read 1990b), so calf survival rates

(p_0) were set as the square of the adult rate, assuming that a calf has the same risk of dying as an adult in addition to the risk of starvation if its mother dies during the calf's first year (Reilly and Barlow 1986). Thus, n_0 values for model A ranged from 0.50 to 0.19.

It is unlikely that the non-calf survival is consant across age classes. Mammalian survival is typically low during juvenile stages, but increases rapidly and then gradually decreases with age (Caughley 1966). Thus, in the second mortality model, model B, we used the smoothed age-frequency (f_x) formula of Caughley's (1966) for Himalayan thar (*Hemitragus jemlahicus*) to estimate n_x values for age classes >0 where

$$(4) \quad \log[f_x] = 1.9673 + 0.0246x - 0.01036x^2$$

at each age x. Sampling of the thar took place during the birth-pulse, and evidence suggested that the sample used for the formula was from a population which had a stationary age distribution and was apparently free of bias (Caughley 1966). Thus the sample was suitable for calculating a life table (Caughley 1977). Under these conditions, $f_{x+1}/f_x = l_{x+1}/l_x$, and we calculated natural mortality of non-calves as $n_x = 1 - f_{x+1}/f_x$.

The life history of thar is similar to that of the harbour porpoise: litter size of one, annual reproduction, and few individuals live past age class 12 (Caughley 1966; Table 1). The most notable difference between the sample c_x of the two species in Table 1 is the relatively low frequency of porpoise calves, but this is due to porpoise calves being underrepresented in the gillnet sample. Thus for model B we allowed n_0 to range from 0.53 (Caughley's (1966) value for thar) to 0.19 (the lower limit of n_0 used in model A).

Incidental mortality rates

We ran each model in the absence of incidental mortality ($h_x = 0$) and at four other levels of incidental mortality. These additional levels were estimated by assuming that the proportions of individuals within all age classes >0 are equally affected by incidental mortality and that these proportions can be represented by dividing minimum and maximum estimates of incidental catches into two estimates of the total population size.

Based on shipboard surveys using line transect techniques, Kraus et al. (1983) produced the most recent minimum estimate of numbers for the Bay of Fundy and Gulf of Maine harbour porpoise population; 7956 ± 1327 (95% CI). Experimental evidence suggested that shipboard surveys recorded only 52% of the porpoises present, so the minimum estimate was corrected to 15 300 ± 2552 (95% CI) (Kraus et al. 1983).

Polacheck (1989) suggested that the annual incidental mortality of this population throughout the year would be at least 280 porpoises, with an upper limit of about 800. These estimates were derived from the following: 130 porpoises killed by gill nets in Canada, 50 killed by other sources including weirs and surface gill nets within Canada and the United States, and 100–600 killed by gill nets in the United States. Data for the United States gillnet component are not as precise as those from Canada because comparable studies of harbour porpoises have not been conducted and because of the "diffuse nature of the fishery" in the United States (Polacheck 1989).

These minimum and maximum estimates of incidental mortality and the two mean population estimates produced the four proportions used in the models as $h_{x>0}$: 0.0183, 0.0352, 0.0523, and 0.1006.

Incidental mortality rates of calves used in the models incorporated an additional component that accounted for their incidental mortality and that of their mothers. We found 30 lactating harbour porpoise females (captured with and without calves) killed incidentally in gill nets in the Bay of Fundy between 1985 and 1988 and 13 calves that were caught alone (unpubl. data). Assuming that lactating females suffer an incidental mortality rate equal to other non-calf porpoises, and that none of the calves caught alone belonged to the lactating females caught without calves, we estimated that h_0 would be greater than the non-calf rate by a factor of (13 + 30)/30; 43 calves would die for every 30 lactating females as a result of incidental catches. This estimate seemed reasonable, since it is unlikely that calves which had lost their mothers in gill nets would dive to the depths that groundfish gill nets are usually set, i.e. we assumed that calves that were caught alone were accompanied by their mothers at the time of capture.

Results

Model A

In the absence of incidental mortality, model A represented a population that would achieve an $r = 0$ (no population increase or decrease) with non-calf n_x rates of about 0.16 and 0.17 using maximum ages of 12 and 15 yr, respectively (Fig. 1). These values correspond to relatively high p_x values of 0.84 and 0.83, respectively. Each level of h_x schedules required lower non-calf n_x rates to achieve an $r = 0$, and at the highest level of $h_{x>0}$ (0.1006), only negative r's are possible at either of the maximum ages used within the parameter limits set for this model.

For an $r = 0$ in the absence of incidental mortality, the proportions of the population in the maximum age classes 12 and 15 in model A were 0.021 and 0.010, respectively. These values are both higher than the proportion of individuals in age classes 12+ from the gillnet sample (0.0092, Table 1), even with the porpoise estimates of age class proportions inflated because of age class 0 being underrepresented. It is questionable, therefore, that harbour porpoise demography can be adequately represented using a model that assumes the same non-calf mortality rate for all age classes.

Model B

In model B, incorporating non-calf thar n_x, r's = 0 were achieved in the absence of incidental mortality with n_0's of approximately 0.41 and 0.42 for maximum ages of 12 and 15 yr, respectively (Fig. 2). At these n_0's, the proportions surviving in the maximum age classes were 0.008 and 0.001, respectively; these values are more reasonable given the empirical data on observed age class proportions of porpoises (Table 1). For the model using a maximum age of 15 yr, the two lower h_x schedules requried n_0's of about 0.35 and 0.27, respectively, to achieve an r of 0 (Fig. 2). Calf natural mortality rates of about 1% less for each level of incidental mortality, respectively, were required using a maximum age of 12 yr (Fig. 2). This model, however, did not produce positive values of r at the two highest levels of non-calf h_x within the limits of n_0 used or either maximum age (Fig. 2).

Discussion

If either model used in this study is a reasonable representation of harbour porpoise demography from the Bay of Fundy

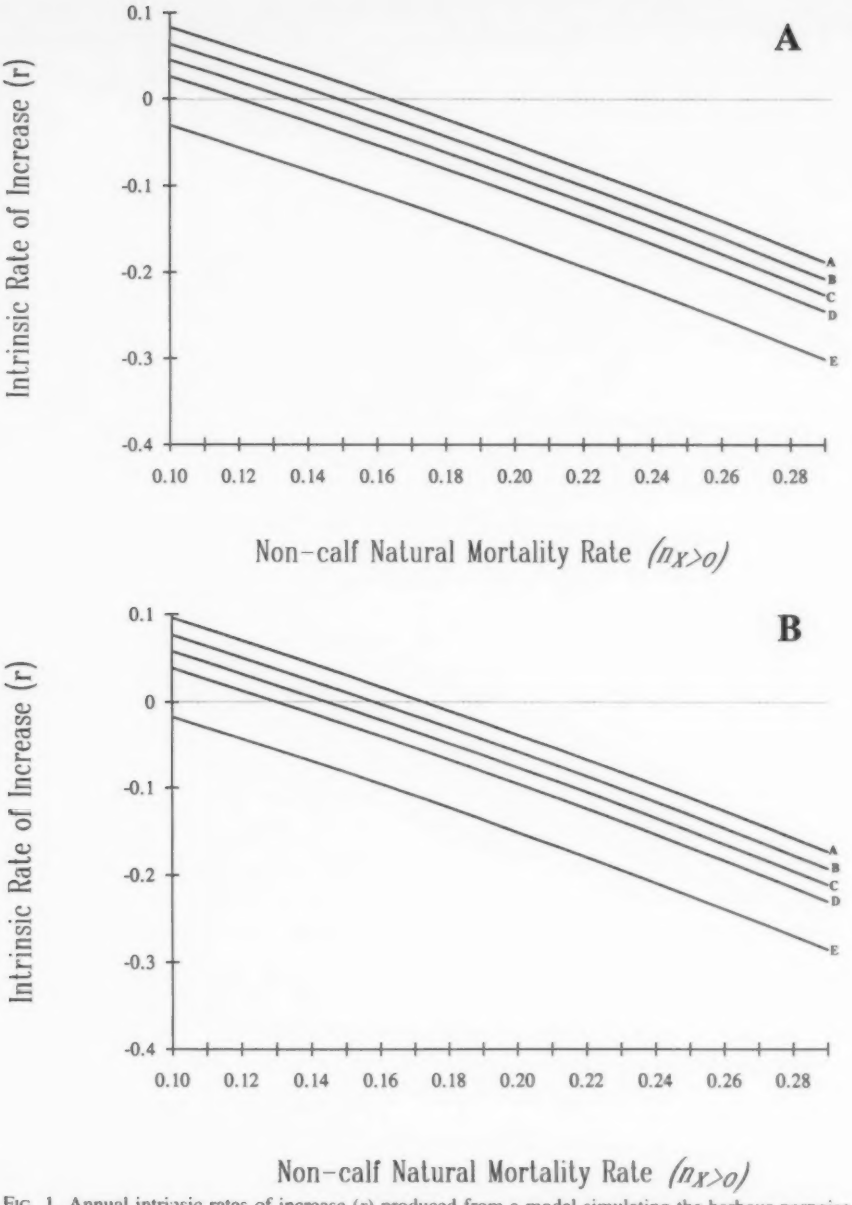

FIG. 1. Annual intrinsic rates of increase (r) produced from a model simulating the harbour porpoise population in the Bay of Fundy and Gulf of Maine, using maximum ages of (A) 12 yr and (B) 15 yr and estimating schedules for rates of reproduction (m_x), natural mortality (n_x), and incidental mortality (h_x) (*A–E*). Non-calf n_x was assumed to be the same for all age classes and ranged from 0.1 to 0.29, while rates of $h_{x>0}$ used are as follows: $A = 0.0000$, $B = 0.0183$, $C = 0.0352$, $D = 0.0523$, and $E = 0.1006$.

and Gulf of Maine, it is unlikely that this population can sustain even moderate levels of incidental mortality. The model which incorporates the most realistic natural mortality schedule, model B, only produced r's = 0 (stable population size) with the two lower schedules of incidental mortality rates (h_x), using maximum ages of 12 and 15 yr. Natural mortality rates of calves (n_0) in these cases were low, ranging from 0.26 to 0.35. For this model to produce an $r = 0$ at the two higher schedules of h_x would require n_0's of less than 0.19. While natural mortality rates of phocoenid claves are not known, such low rates are unlikely to occur in nature. Caughley (1966) indicated a first year class mortality rate for female thar of about 0.53. In the absence of incidental mortality, model B required calf natural mortality rates of 0.41 and 0.42, respectively, to maintain stable population sizes with maximum ages of 12 and 15 yr.

The ability of harbour porpoise populations to withstand incidental mortality is constrained by their life history. Like Himalayan thar, harbour porpoises can produce only a single

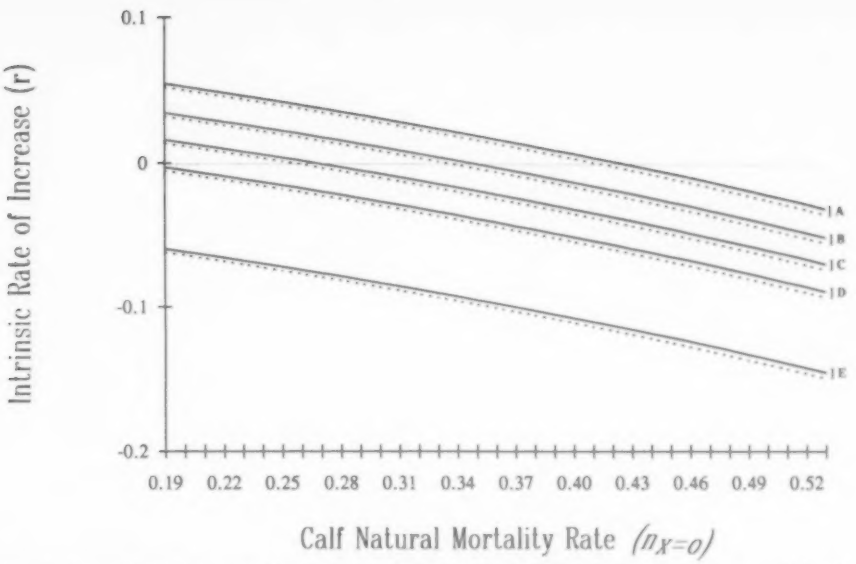

FIG. 2. Annual intrinsic rates of increase (r) of a model simulating the harbour porpoise population in the Bay of Fundy and Gulf of Maine, using maximum ages of 12 yr (broken lines) and 15 yr (solid lines) and estimating schedules for rates of reproduction (m_x), natural mortality (n_x), and incidental mortality (h_x) (A–E). Non-calf n_x's were calculated for each age class from the smoothed age-frequency formula for Himalayan thar from Caughley (1966), while rates of $h_{x>0}$ used are as follows: $A = 0.0000$, $B = 0.0183$, $C = 0.0352$, $D = 0.0523$, and $E = 0.1006$.

offspring from each pregnancy (Caughley 1966; Read 1990a). Caughley's (1966) data, however, show that female thar attain sexual maturity almost a year earlier than harbour porpoises (Read 1990a) and that some thar live past 15 yr of age. This combination of late maturation and short life span in harbour porpoises limits the net reproductive rate of individual females and prevents the population from achieving high rates of increase.

The substantial decrease in calf natural mortality required for model B to represent a stable population once incidental mortality was included (Fig. 2) is particularly interesting given the recent changes in calf size documented by Read and Gaskin (1990). Harbour porpoise calves examined in the Bay of Fundy between 1985 and 1988 were significantly larger than those taken from 1969 to 1973, prior to the establishment of the commercial groundfish gillnet fishery. Read and Gaskin (1990) suggested that this larger calf size reflected an increase in maternal investment and speculated that larger calves might have a better chance of surviving their first year. Indeed, model B indicates that a dramatic decline in calf natural mortality would allow the population to withstand incidental mortalities.

There are several potential biases in the analysis, but they do not weaken our major conclusions. First, it is clear that the age class proportions of the porpoise sample from gill nets in Table 1 are biased; there are very few calves in the sample. Such biases, however, do not influence the estimation of reproductive rate or fecundity data (Caughley 1977). The age-specific reproductive rates, m_x, used in the models were derived from pregnancy rate data and thus overestimate actual values because, as is mentioned above, they do not account for unsuccessful implantation, abortion, or foetal resorption. Females may also exhibit some degree of reproductive senescence, where reproductive rates decline at older ages (Eberhardt 1985), and we did not consider this in our models (Table 1). Thus, the actual m_x values of porpoises are likely lower than those we used, and the true rates of increase would be lower for any specific natural mortality schedule.

The estimates of the proportions of the population killed incidentally in fishing gear are also questionable. It is likely, however, that the rates used in this analysis are conservative, particularly in our value for the lower limit of incidental catches (280 per year). The upper limit of incidental mortality used in this analysis (800) is probably the most realistic and produced negative rates of increase within the parameter bounds used in both models. Incidental catches of harbour porpoises in other areas of the Gulf of Maine are not included in this upper limit (Polacheck 1989), such as those which occur off southwest Nova Scotia (Read and Gaskin 1988), so the actual number of incidental mortalities may even be greater than 800.

We may also have underestimated the potential longevity of harbour porpoises in the models. As was noted by Read (1990a), however, many other researchers have reached similar conclusions; very few harbour porpoises in any population live to 12 yr of age or older. These researchers have used a variety of age estimation techniques and collected samples from strandings, incidental catches, and hunting. Further, increasing the maximum age from 12 to 15 yr in the models produced only a small change in the rate of increase. In model A, non-calf natural mortality rates which were required for a stable population size ($r = 0$) increased by about only 1% with the increase from 12 to 15 yr (Fig. 1). Similarly, calf natural mortality rates required for population stability in model B increased by about only 1% with the greater maximum age (Fig. 2). Given that we have never encountered a porpoise older than 15 yr, and that few individuals live longer than 8 yr (Gaskin et al. 1984; Read 1990b), it is unlikely that we have underestimated the life span

of harbour porpoises. Indeed, Barlow and Boveng (1991) suggested that a "longevity" (99th percentile of the age distribution of a sample) of 10 yr is more appropriate for harbour porpoise models.

Additionally, there are uncertainties about the structure of this harbour porpoise population. Based on indirect evidence from the timing and distribution of sightings, strandings, and incidental catches, Gaskin (1984) suggested that harbour porpoises in the Bay of Fundy and Gulf of Maine formed one of four population units in the western North Atlantic. The other populations described by Gaskin (1984), however, are also subjected to incidental mortalities of unknown magnitude in gillnet fisheries within the Gulf of St. Lawrence, off Newfoundland and Labrador, and the west coast of Greenland (Lear and Christensen 1975; Lien 1987; Fontaine et al. 1990).

It is possible that smaller, more discrete population units may exist within the Bay of Fundy and Gulf of Maine. Given that gill nets in this region are generally set in shallow waters close to shore (Read and Gaskin 1988), an inshore component of the population would be subjected to a higher proportion of incidental mortalities than we used in the models. The models presented here indicate that if this were the case, such population "units" would decline.

Although our models indicate that gillnet fisheries may be having a negative impact on harbour porpoises in the Bay of Fundy and Gulf of Maine, management options to mitigate the impact of gillnet fisheries are limited. Experimental work to make monofilament gill nets more "visible" to the echolocation of dolphins and porpoises has not resulted in reduced catches (Hembree and Harwood 1987; Au 1990). Porpoises may actually be attracted to the nets because of the struggling fish and scavenger activity; odontocetes may lose "sight" of the net once their echolocation has focused on a prey item with a much higher target strength (Goodson and Klinowska 1990). Although other gear modifications and deployment techniques should be investigated, their effectiveness in reducing harbour porpoise incidental catches, while not reducing fish catches, does not appear promising.

More effective management options may include temporal or spatial restrictions of gillnet use, or a switch to gear types that do not lead to incidentally mortalities of harbour porpoises. Most fishers are averse to such management options because of the potential economic hardship that they may have to endure. Indeed, the relative efficacy of conservation measures should be evaluated with respect to their potential for reducing incidental mortalities while minimizing costs to individuals in the gillnet fishery.

In conclusion, we wish to restate the findings of Barlow (1986); harbour porpoises appear to have a very limited ability to withstand incidental mortality and should be managed conservatively. The decline of other harbour porpoise populations (Gaskin 1984) serves as a reminder of the vulnerability of this species. The results of our simple models indicate that immediate action should be taken to reduce the level of incidental catches in the Bay of Fundy and Gulf of Maine.

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Does Tagging and Handling Affect the Growth of Northern Fur Seal Pups (*Callorhinus ursinus*)?

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Trites, A. W. 1991. Does tagging and handling affect the growth of northern fur seal pups (*Callorhinus ursinus*)? Can. J. Fish. Aquat. Sci. 48: 2436–2442.

From 1957 to 1966, samples of tagged and marked northern fur seal pups (*Callorhinus ursinus*) consistently weighed less than untagged and unmarked pups on the Pribilof Islands, Alaska. At the time, it was concluded that tagging and handling had caused a loss of weight and had slowed the normal rate of pup growth. In re-evaluating the data from this time period, it seems that tagged pups grew at the same rate as untagged pups, but were smaller at the time of tagging than average size pups. The growth curve for tagged pups appears to lag behind that of untagged pups, suggesting that tagged pups were born later in the breeding season and were more susceptible to being captured and tagged than older and heavier pups.

De 1957 à 1966, des échantillons de jeunes otaries à fourrure (*Callorhinus ursinus*) des îles Pribilof, Alaska, révélaient que le poids des animaux étiquetés et marqués était constamment inférieur au poids des animaux sans marque ni étiquette. On avait alors conclu que l'étiquetage et la manipulation des jeunes otaries avaient causé une perte de poids et un ralentissement de leur croissance. Une nouvelle analyse des données semble toutefois indiquer que le taux de croissance était le même pour les animaux, qu'ils soient étiquetés ou non; cependant, les animaux étiquetés avaient une taille inférieure à la moyenne au moment de l'étiquetage. En effet, la courbe de croissance des animaux étiquetés est décalée par rapport à celle des animaux non étiquetés, ce qui laisse croire que les animaux étiquetés sont nés plus tard au cours de la période de reproduction; ils étaient de ce fait plus faciles à capturer et à étiqueter que leurs congénères plus âgés et plus lourds.

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In 1957, northern fur seal pups (*Callorhinus ursinus*) were weighed a few weeks after tagging and found to be lighter than untagged pups (Abegglen et al. 1957). Over the next 9 yr, biologists continued to report that untagged pups outweighed tagged pups on the Pribilof Islands, Alaska (Roppel 1984). Their conclusion was "tagging, marking, and handling, individually or combined, causes a loss of weight or slows the normal rate of weight gain. Loss of weight may cause tagged or marked pups to die at a greater rate than untagged and unmarked pups during their first winter at sea, thus inflating later estimates of the population based on recoveries of tagged and marked seals" (Marine Mammal Biological Laboratory 1969, p. 13).

Research into the effect of tagging and handling on the growth of northern fur seal pups ended in 1966 as interest in tagging seals waned. Biologists began expressing renewed interest in tagging in the mid-1980s (see Fowler 1986) and have been applying tags to samples of pups on the Pribilof Islands since 1987 to evaluate early survival, tagging procedures, and the longevity of different types of tags (G. A. Antonelis, (National Marine Mammal Laboratory (NMML), Seattle, WA, pers. comm.). The possibility that handling pups might slow growth and reduce future survival has implications for pinniped studies that rely on marking individuals for future identification. It also has bearing upon the interpretation of historical data collected from tagged northern fur seals and is relevant to understanding whether the mark–recapture method for estimating the number of pups born is detrimental to the survival of the Pribilof population. Could the shearing of thousands of pup heads (see York and Kozloff 1987) be reducing the young animals' growth rates and future survival?

The goal of my study is to reassess the data collected on tagged and untagged pups from 1957 to 1965 to determine whether tagging affects pup growth. A second goal is to reexamine data collected during 1965–66 from pups that were marked but not tagged to see whether the type of marking is related to pup growth. I begin by reviewing the methods used to tag and, later, to weigh the pups. I then compare the weights of tagged and marked pups and test whether tagged pups actually grew at a slower rate than untagged pups.

Materials and Methods

Tagging, Marking, and Weighing

Fur seal pups are born between the last week of June and the end of July (Bartholomew and Hoel 1953; Peterson 1968). The number of births over time is positively skewed, with over 50% occurring during the first 2 wk of July (Bartholomew and Hoel 1953; Peterson 1968; Trites 1992). By early August, the pups from large aggregations, gathering in areas where they are least likely to be trampled by the bulls. As the month progresses the pups being to play in and near the water's edge. On average, pups were about 5–6 wk old when tagged in mid-August and 7–8 wk old when weighed from August 29 to September 3.

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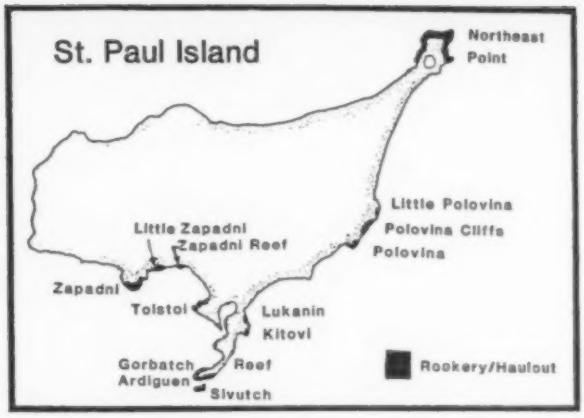

FIG. 1. Rookery sites on St. Paul Island, Alaska (adapted from Lander 1980).

Tagging and weighing were conducted between 1957 and 1966 on St. Paul Island, Alaska, by the United States Fish and Wildlife Service. Methods of data collection are contained in the annual "Fur Seal Investigations" reports (e.g. MMBL 1969) published by the United States Fish and Wildlife Service and are summarized as follows.

From 1957 to 1965, monel metal cattle-ear tags were applied at the hairline on the front flipper (1957–64) or between the fourth and the fifth digit (1964–65). Checkmarks, used to identify pups that lose the tag, were made by cutting a V-notch near the tip of a flipper or by slicing off a flipper tip. Tags were allotted to each rookery according to the proportion of harem bulls counted on that rookery. From 1957 to 1962, approximately 10 000 pups were annually tagged at each of Northeast Point and Reef rookeries (see Fig. 1 for locations). Fewer pups were tagged each year at Polovina (4400) and Zapadni Reef (3500). There was a further drop in the number of tags annually attached from 1963 to 1965 (2400 at Reef; 2500 Northeast Point; 1000 Polovina; 900 Zapadni Reef). In all, approximately 200 000 pups were tagged at these four rookeries on St. Paul Island between 1957 and 1966.

The aggregations of pups on the rookeries were approached from the inland side and herded towards barricades set up behind the rookery away from the water. The pups were lifted onto tables, tagged, and released seaward of the barricades. Some areas were covered more than once to achieve the desired number of tagged seals.

Information on the effect of handling as opposed to tagging was obtained in two years. In 1965, some untagged pups were marked by removing the tip of the first digit on the right hind flipper and were weighed 12–14 d later (Roppel et al. 1966). In 1966, 800 pups on Zapadni Reef and an equal number at Northeast Point were marked by shearing a patch of fur from the rump. They were weighed 13 d after marking (MMBL 1969).

Pups were weighed on a spring scale in the early years and later on a platform scale (Roppel et al. 1966). While the technique for weighing the pups was refined over the years, it remained consistent within years such that tagged and untagged pups were weighed under identical conditions in any given year.

For weighing, pups were rounded up and herded towards barricades. Pups were chosen for weighing from the "mob" that ensued and were released beyond the enclosure to prevent

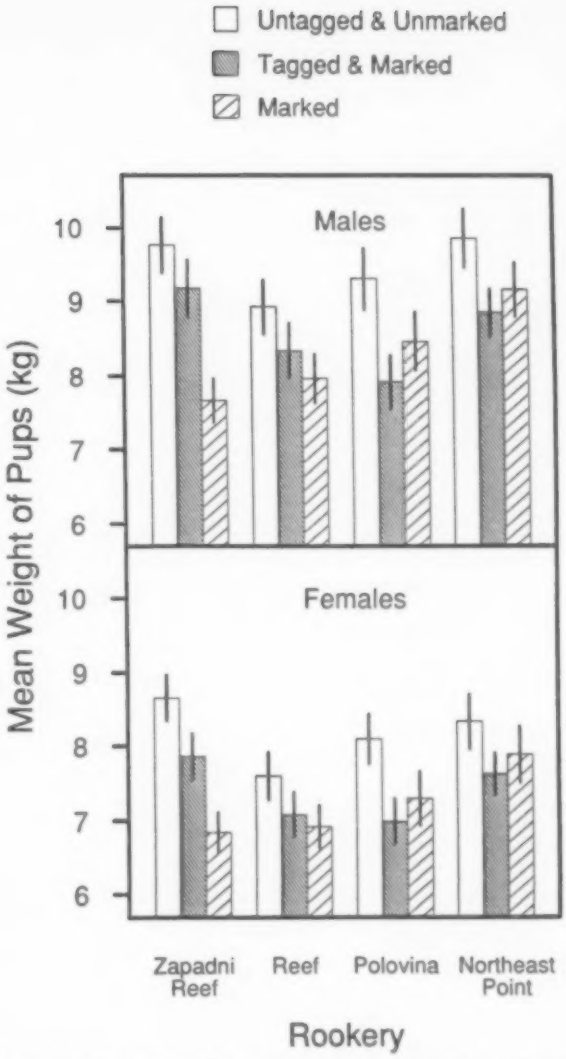

FIG. 2. Mean body weights of the tagged, marked, and untagged/unmarked pups weighed on four rookeries on September 2–3, 1965. Untagged pups were always heavier than those tagged and marked. Similarly, males weighed more than females. The solid lines show the 95% confidence intervals for the estimated mean weights.

reweighing. From 1957 to 1961, the annual number of tag-bearing pups weighed on a rookery varied between 1 and 111 of each sex and averaged about 50. The number of untagged pups also varied during the same period, averaging about 100 animals of each sex. From 1962 to 1966, biologists annually weighed 75 tagged and 75 untagged pups of each sex. In all, approximately 3500 tagged and 5500 untagged pups were weighed between 1957 and 1966.

The pup weight data are summarized in the annual "Fur Seal Investigation" reports and were obtained on magnetic tape from NMML, Seattle, WA.

Analysis of Growth Patterns

The mean weights of male and female pups (untagged, marked, and tagged) were estimated for each rookery and year

when more than 30 pups were weighed. Differences between the mean weights of tagged and untagged pups were then determined and 95% confidence intervals calculated. Weights of marked, tagged, and untagged pups recorded in 1965 were also reexamined and tested, by analysis of variance, to determine whether changes in weight were related to the type of mark applied.

The effect of tagging on growth was considered in three ways. First, the mean weights of tagged pups were compared with the mean weights of untagged pups. Next, the relative difference in weights ([untagged − tagged]/untagged × 100%) was plotted against the number of days elapsed since tagging to see whether or not a relationship could be attributed to the effects of tagging. Finally, growth curves were constructed for tagged and untagged pups and compared with one another.

Growth curves were drawn for two different time periods. The first was a reanalysis of three weighings of tagged and untagged pups made a month apart in 1962 that began 1 wk after tagging (Roppel et al. 1963). The second growth curve pooled the mean weights of pups recorded on each rookery from 1958 to 1966 and plotted them against the day they were made (between August 29 and September 3). Separate linear regressions were fit to the tagged and untagged data sets. The equality of the two population regression coefficients was determined with a Student t-test (Zar 1984). If the slopes (i.e. growth rates) were not statistically different, a second t-test was applied to determine whether the elevation (i.e. the vertical position) of the parallel growth curves differed significantly (Zar 1984).

Results and Discussion

Marked and tagged pups weighed in 1965 were lighter than previously unhandled pups (Fig. 2). But there does not appear to be a significant difference between the mean weights of marked pups and tagged pups. The weights of marked and tagged females were not significantly different on each of the four rookeries ($F_{1,588} = 1.767$, $p = 0.184$). For males, the difference in weight ($F_{1,588} = 4.039$, $p = 0.045$) is attributed to the Zapadni Reef sample. There was no significant difference in the mean weights of marked and tagged males among the other three rookeries ($F_{1,441} = 1.122$, $p = 0.290$). Thus, since the type of mark (either tagging or slicing the flipper tip) does not appear to be correlated with the weight of the pup, the remainder of this paper refers to all marked and tagged pups as being tagged.

With few exceptions, the mean weights of pups not previously handled or tagged consistently exceeded the mean weights of tagged individuals on all rookeries (Fig. 3 and 4). In some years the difference in weights between the two groups was as much as 1.7 kg, but there was no consistent pattern among the

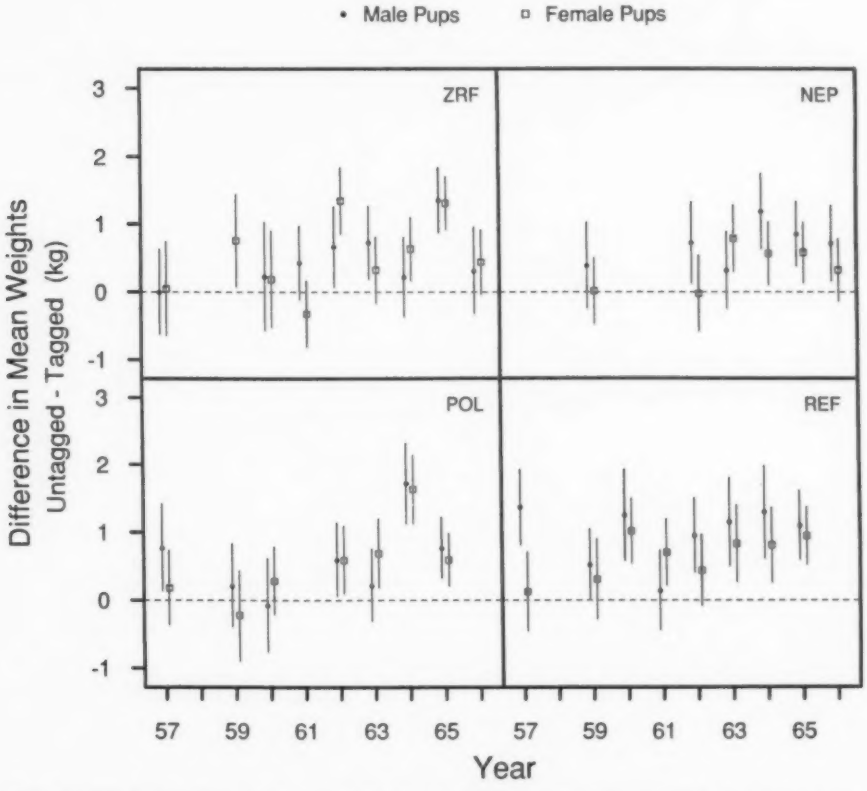

FIG. 3. Annual differences in the mean body weights of tagged and untagged male and female pups weighed on four rookeries: Zapadni Reef (ZRF), Northeast Point (NEP), Polovina (POL), and Reef (REF). Most of the points lie above the broken line of no difference, indicating that untagged pups weighed more than tagged pups. Solid lines are 95% confidence intervals for the estimated difference in mean weights.

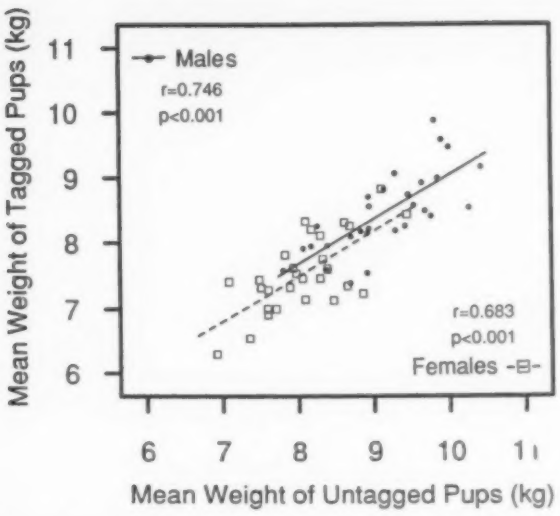

FIG. 4. Mean weights of tagged pups versus those without tags. Each point represents one rookery and one year (mean weights were calculated for samples sizes greater than 30 pups). The significance of the linear regressions is shown at the top and bottom of the panel for males and females, respectively. The different elevation of the parallel regressions shows the size difference between males and females.

different rookeries (cf. York and Antonelis 1990a, 1990b). Considerable variability existed among sexes. In some years, and on some rookeries, the difference between the weights of tagged and untagged pups was the same for both males and females. At other times and places (e.g. Reef, 1957, Fig. 3) there was a marked difference between the apparent effect of tagging on males and females.

Growth Rates

In 1962, tagged and untagged pups were weighed on three occasions: September 2–3, October 2–3, and October 24–25 (Fig. 5). Roppel et al. (1963) applied a *t*-test to each pair of observations according to date and rookery. They concluded that weight differences within rookeries were significant at the first weighing but were insignificant at the third weighing. In other words, they concluded that the immediate weight loss caused by tagging was partially overcome after 2 mo.

The lack of significance between the weights of tagged and untagged pups at the third weighing is partly explained by the small sample sizes and by the large variation in body weight attributable to growth. Pooled estimates of the standard deviation of male weights increased between the successive weighing periods from 2.00 to 2.46 to 2.98 kg. The standard deviations of female weight on the three occasions were 1.64, 2.12, and 2.41 kg. Sample sizes of 75 were sufficient on the first day of weighing to detect differences as small as 0.75 kg between the weights of tagged and untagged females, but should have been increased to 112 and 144 on the second and third weighings to maintain the power of the *t*-test (when $\alpha = 0.05$, $\beta = 0.25$). The sample size necessary to detect the same weight difference among tagged and untagged males should have been 95, 150, and 220 pups for each successive weighing. Thus it cannot be concluded with assurance that tagged pups regained their weight loss 2 mo after tagging because the probability of

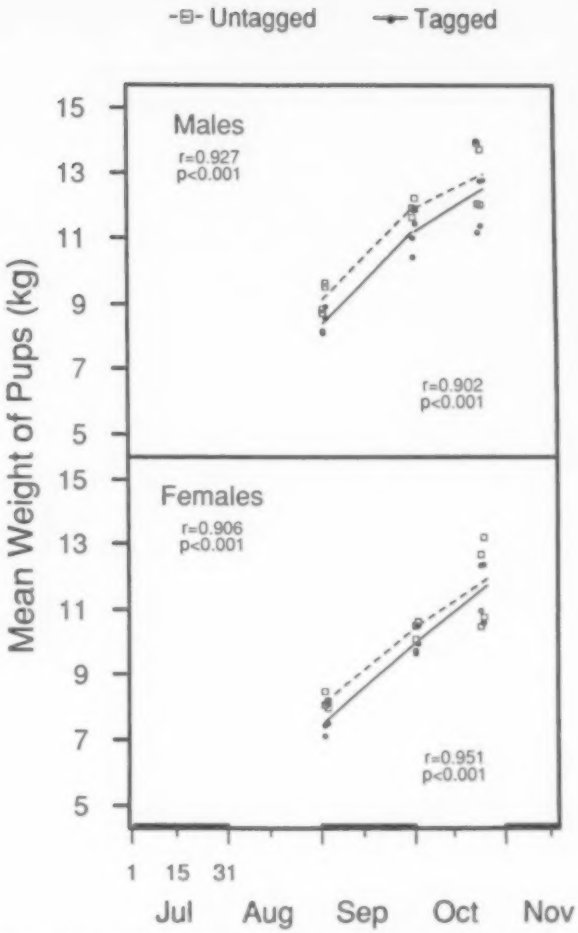

FIG. 5. Mean body weights of male and female pups weighed on four rookeries from September to October 1962. Linear regression describe two periods of growth for tagged and untagged pups. The significance of the separate regressions are contained in Table 1, while the significance of a single regression of the weight of pups over the three time periods is shown in the top and bottom of each panel, respectively.

detecting a true difference among the mean weights of tagged and untagged pups on the third weighings was too small (i.e. β, the probability of not rejecting the null hypothesis when it was in fact false was greater than 0.80).

Fitting linear regression to the 1962 data, pooled from all four rookeries, suggests that tagged pups grew at the same rate as untagged pups over the periods September 2 to October 3 and October 2–24, but were smaller than average when tagged (Fig. 5; Table 1). The same conclusion is drawn from growth curves constructed for the 6-d period August 29 to September 3 (Fig. 6; Table 1). It seems that both groups of pups started out in time at different sizes.

Unlike the weights of tagged males, tagged females, and untagged females shown in Fig. 6, the linear regression of untagged male weights from August 29 to September 3 was not significant because of the large variance associated with the larger male body weights. A significant relationship occurs when the number of data points is increased by including untagged males weighed in 1967–71, 1984, and 1987 ($F_{1,55}$ =

TABLE 1. Linear regression coefficients (growth rates) estimated for tagged and untagged pups weighed in 1962 and 1957–66. The equality of the two population regression coefficients was tested with a Student t-test (t_{slope}). A second t-test was used to test whether the elevations of the two population regressions were the same ($t_{elevation}$). The probabilities associated with the sample statistics are enclosed in parentheses. The rate of growth from 1957 to 1966 was determined using the annual mean estimates of body weights from each rookery where at least 30 pups were weighed.

Time period			Growth rate ($kg \cdot d^{-1}$)				
Year(s)	Days	Sex	Tagged	Untagged	t_{slope} (p)	$t_{elevation}$ (p)	Sample size
1957–66	Aug. 29 – Sept. 3	M	0.179	0.131	0.432 (0.334)	−4.307 (<0.001)	56
		F	0.180	0.160	0.214 (0.416)	−4.005 (<0.001)	58
1962	Sept. 2 – Oct. 3	M	0.093	0.092	0.120 (0.452)	−5.768 (<0.001)	1191
		F	0.081	0.077	0.544 (0.293)	−4.864 (<0.001)	1194
1962	Oct. 2–25	M	0.057	0.046	0.742 (0.229)	−3.547 (<0.001)	1191
		F	0.073	0.061	0.952 (0.171)	−2.517 (0.006)	1196

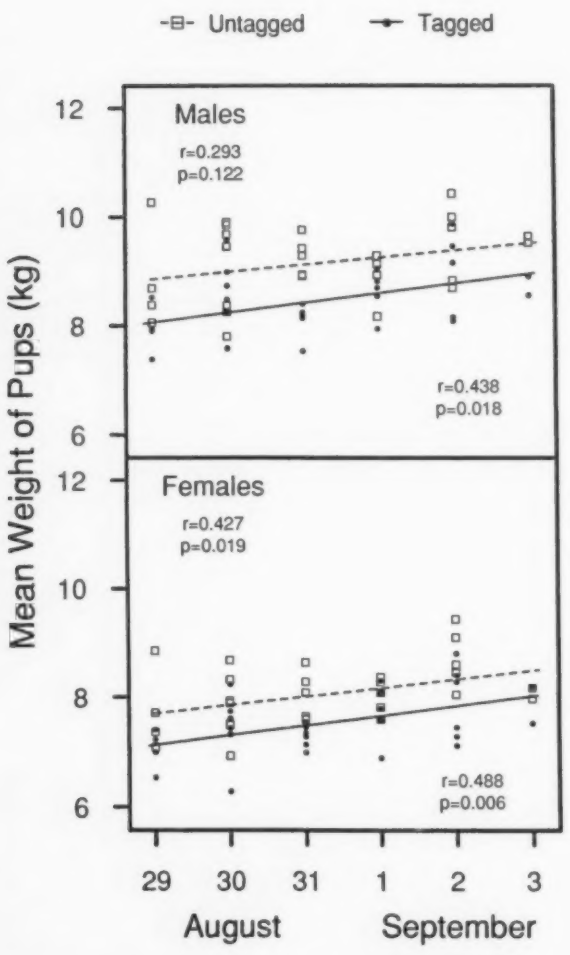

FIG. 6. Mean body weights of tagged and untagged pups weighed from August 29 to September 3. Each point represents one rookery and one year from 1957 to 1966 where the sample size was greater than 30. The linear regressions were fit to the mean data points rather than the raw values to reduce the combined effect of annual differences in body weights and sample sizes. The significance of the regressions is shown in the top and bottom of each panel.

4.97, $p = 0.030$; unpubl. data from the files of NMML, Seattle, WA). The slope of this regression (the growth rate) was not significantly different from the slope for tagged pups ($t_{83} = 0.486$, $p = 0.314$), but the regression elevations did differ ($t_{83} = -5.974$, $p < 0.001$).

The growth rate of males and females slows from August to November during the moulting period. For untagged males, the growth rate decreased from 0.131 to 0.092 to 0.046 $kg \cdot d^{-1}$ as the season progressed (Table 1). This reduced growth rate may reflect a decline in the amount of energy that a mother can transfer through her milk to her growing pup, or it may be that the metabolism of pups increases more rapidly with body size than does feeding rate. The duration of female feeding trips at sea (absence from the rookery) is known to increase over the breeding season and is believed to reflect the nutritional needs of the pup (Gentry and Holt 1986) Presumably, milk cannot meet the needs of a growing pup for more than about 4 mo, and it becomes necessary for the pup to increase its energy intake with solid foods.

Curiously, the growth rates of tagged pups, although not statistically different, always exceeded the growth rate of untagged pups (Table 1). If there was no difference in the growth rate, there should be an even distribution of the slopes, half (on the average) being greater for one group compared with the other. But all six cases fall in the same pattern which, from a binomial view of the probability, would occur with a chance of only 0.016. Some might therefore conclude that tagging increases the growth rate. A more likely explanation, however, is that tagged pups were born later than untagged pups and hence were in a different growth phase, or that the growth curve of tagged pups lagged behind that of untagged pups, or both.

If tagging had a persistent effect on growth, then there should be a relationship between the size of the pup and the number of days elapsed since tagging (Fig. 7), but there is none. It therefore appears, based on this and the above evidence, that tagging and handling did not affect pup growth, but that the pups selected for tagging were smaller than average and hence were not representative of the whole population. Conceivably, the pups rounded up for tagging were born late in the season. Perhaps many pups born earlier were in the surf and tide pools at the time of tagging and could not be rounded up. Or perhaps pregnant females that returned to land later in the breeding season were forced to give birth in the low-density peripheral regions of the rookery, such that their pups were more susceptible to being captured. Furthermore, taggers may not have chosen pups at random from the numbers they rounded up. Pups tend to pile up (and even smother) when surrounded. Perhaps

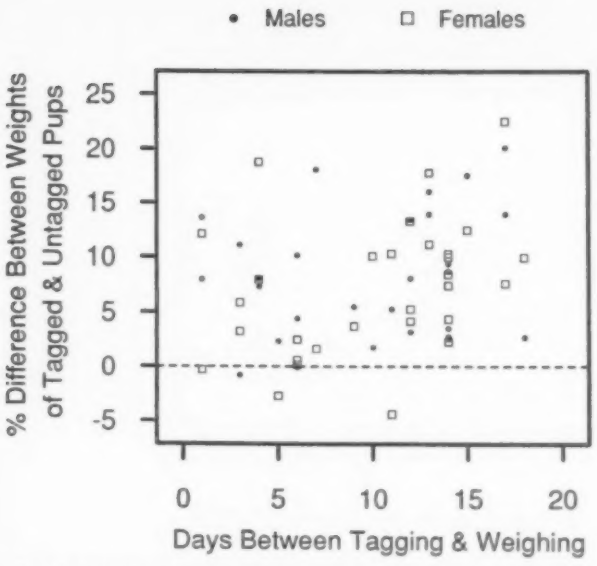

FIG. 7. Relative differences between the mean body weights of tagged and untagged pups subsequent to tagging. Each data point shows how much heavier untagged pups were compared with tagged individuals (expressed as a percent of tagged body weight). Each value represents the mean relative difference in body weights for one rookery and one year from 1958 to 1966. Dates of tagging were not available for 1957. There appears to be no relationship between the effect of tagging and the number of days elapsed since tags were attached.

smaller pups were taken from the top of the piles, leaving the heavier pups at the bottom.

There are a number of cases reported in which tagged (or marked) pups have been found to be lighter that the remaining seals at the time of marking. In one study, Roppel et al. (1981) followed a shearing crew that moved through the breeding beach to mark pups by shearing a patch of fur from the top of the pups' heads. The authors found that pups selected for shearing were lighter than unsheared pups and concluded that smaller pups were easier to handle. Another study by Gentry and Francis (1981) of known-aged animals concluded that pups captured for shearing were younger than noncaptured pups. Further evidence of this sampling bias is contained in Fig. 3 which shows a larger weight difference for males than females in 20 of 29 comparisons (binomial probability $P(X \geq 20) = 0.012$). This observation is again consistent with a sampling bias for selecting small pups at the time of tagging, given that males are on average heavier than females.

Other Species

Tagging pinnipeds facilitates studies of life history, population biology, behaviour, growth and development, dispersal from rookeries, and fidelity to birth sites. It also permits validation of aging techniques based on teeth (Condy and Bester 1975; Summers and Witthames 1978). Despite the tagging of many species of fur seals (e.g. Rand 1950, 1959; Csordas and Ingham 1965; Bonner 1968; Crawley and Brown 1971; Stirling 1971; Laws 1973; Condy and Bester 1975; Payne 1979; Mattlin 1981; Kerley 1985), there is little or no information about the possible effect that tagging might have on pup growth. Observations of Antarctic fur seals (*Arctocephalus gazella*) led Payne (1979) to suggest that pups tagged within 1 mo of birth grew slower than untagged pups, although no data were presented. Further studies of Antarctic fur seal pups, tagged when 2 mo old, showed no abnormal growth rates (Kerley 1985), not did tagged New Zealand fur seal pups (*A. forsteri*) (Mattlin 1978, 1981). Possibly the tags did not alter growth because they were attached at a less critical time in the development of the pup (Kerley 1985). On the other hand, it should be noted that none of the authors presented their data and that their conclusions appear to be based on small sample sizes. Thus it is doubtful that differences between the mean size of tagged and untagged pups could have been detected had they actually been present.

Results from reassessing pup weight data from northern fur seals suggest that tagging too early does not alter growth rates, but results in selecting individuals that are smaller than average. Possibly, pups of different ages are not randomly distributed on the rookery during the first month of pupping, but are segregated by size, such that small pups are more easily accessible for tagging and weighing than are larger ones.

While I do not believe that the weight differences between tagged and untagged pups are due to the tag, they are clearly nonetheless real and associated with tagging. This may well affect the relative survival of tagged pups in their first winter (or at any other time) and hence the validity of the assumptions of mark–recapture analysis. Thus the conclusions quoted from MMBL (1969) in the opening paragraph may be quite valid, if for the wrong reasons.

The conclusion that tagging and handling do not significantly affect pup growth can be strengthened or weakened by weighing pups at the time of tagging, recording their tag numbers, and then resampling at later dates to compare changes in body weight. This would undoubtedly reveal some of the possible biases inherent in the sampling design and shed light on the biological factors that cause differences in average weight. Researchers must be aware of the large variances in body weight and the difficulty of recapturing marked animals and therefore take statistically large samples to detect any changes in body size. This kind of research should be done before committing resources to long-term tagging programs.

Acknowledgements

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Changes in Plasma T_4 and T_3 Levels during Reconditioning and Rematuration in Male and Female Wild Atlantic Salmon (*Salmo salar*) Kelts Held in Freshwater under Two Photoperiod Regimes

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The plasma level of L-thyroxine (T_4) of wild reconditioned Atlantic salmon (*Salmo salar*) kelts held in freshwater at seasonal temperatures on a natural simulated photoperiod showed a robust seasonal profile with a marked peak in early spring followed by low levels throughout the summer. Plasma T_4 was low in kelts that did not recondition and was uninfluenced by gender, eventual reproductive state, or imposition of a 6-mo compressed photocycle. The plasma 3,5,3′-triiodo-L-thyronine (T_3) level also rose in spring in both males and females. In males and nonreproducing females, plasma T_3 remained high during the growth phase in summer and decreased in fall and winter. Plasma T_3 was very low in nonfeeding fish and showed some influence by the 6-mo compressed photocycle. Plasma T_3 was particularly low in females at the time of vitellogenesis when 17β-estradiol was high. It is concluded that in reconditioned Atlantic salmon kelts, levels of plasma T_4 and T_3 appear to be controlled independently and that plasma T_3 is more susceptible than T_4 to vitellogenic state and other factors relating to metabolic demands.

Le taux plasmatique de la L-thyroxine (T_4) chez des charognards sauvages reconditionnés du saumon de l'Atlantique (*Salmo salar*) gardés en eau douce, à température saisonnière et photopériode naturelle simulée, montre un profil saisonnier robuste présentant un pic prononcé au début du printemps et des concentrations faibles au cours de l'été. La T_4 plasmatique a été faible chez les charognards non reconditionnés et n'a pas varié en fonction du sexe, de l'état reproductif final ou de l'imposition d'un photocycle comprimé de 6 mo. La concentration plasmatique de 3,5,3′-triiodo-L-thyronine (T_3) s'est également accrue au printemps chez les mâles et les femelles. Chez les femelles qui ne se reproduisent pas et chez les mâles, la T_3 plasmatique est demeurée élevée pendant la phase de croissance de l'été, puis a chuté en automne et en hiver. La T_3 plasmatique a été très faible chez les poissons ne s'alimentant pas et a varié quelque peu en fonction du photocycle comprimé de 6 mo. La T_3 plasmatique a été particulièrement faible chez les femelles au moment de la vitellogenèse correspondant à une concentration élevée de 17β-œstradiol. En conclusion, il semble que chez les charognards reconditionnés du saumon de l'Atlantique, les concentrations de T_4 et de T_3 plasmatiques sont régulées indépendamment et que la T_3 plasmatique est plus affectée que la T_4 par l'état vitellogénique et par d'autres facteurs liés aux besoins métaboliques.

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Atlantic salmon (*Salmo salar*) are capable of spawning more than once, but in nature only 5–10% return from the sea to freshwater to spawn a second time (Gray et al. 1976). This low return of second spawners represents a considerable loss of reproductive potential. A much higher survival (80–95%) was achieved when postspawned Atlantic salmon (kelts) were retained in captivity in freshwater (Ducharme 1972; Gray et al. 1976, 1987; Hill 1978; Johnston et al. 1990). However, the spawning success of these reconditioned kelts was only 40% for females in their first year of captivity. Recently it was shown that reconditioning and rematuration of Atlantic salmon kelts could be manipulated with two 6-mo compressed light cycles and warm water temperatures in the winter and that 100% maturation could be achieved in females (Johnston et al. 1990). Although the conditions did not enhance reproductive function in the first year in captivity, the length of the reproductive cycle in the second year was shortened by approximately 6 mo and spawning occurred in the spring when daylength was increasing.

To date, the endocrine changes underlying the reconditioning and rematuration processes of Atlantic salmon kelts have not been studied. Such information is required if the regulation of the reconditioning process is to be understood and the reconditioning enhanced. As a first step in this direction, we report here on the plasma levels of the thyroid hormones (TH L-thyroxine (T_4) and 3,5,3′-triiodo-L-thyronine (T_3) from many of

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the specimens used in the aforementioned reconditioning study, in which photoperiod was manipulated to improve reproductive success (Johnston et al. 1990). The activities of several endocrine systems undoubtedly change during kelt reconditioning. However, TH were chosen because in salmonids they undergo major seasonal changes, which in several instances are correlated with energy availability, growth, and reproductive status (White and Henderson 1977; Osborn et al. 1978; Leatherland and Sonstegard 1980; Pickering and Christie 1981; Sower and Schreck 1982; Biddiscombe and Idler 1983; Ueda et al. 1984; Cyr et al. 1988a; Dickhoff et al. 1989; Leatherland et al. 1989). In support of these correlative data, several experimental studies have shown that thyroidal status depends on nutrient intake (Eales 1988) and that thyroidal status may in turn contribute to regulation of somatic growth (Higgs et al. 1982), early oocyte development (Hurlburt 1977; Dettlaff and Davydova 1979; Epler and Bieniarz 1983; Sen and Bhattacharya 1981; Cyr and Eales 1988a, 1988b), and also oocyte final maturation (Pickering and Christie 1981; Sullivan et al. 1989; Dickhoff et al. 1989; Norberg et al. 1989).

The specific objectives of this study were to describe the seasonal changes in plasma T_3, T_4, T_4/T_3 ratio, and 17β estradiol (E_2) levels in fed postspawned Atlantic salmon held in freshwater at seasonally fluctuating water temperatures under either a simulated natural photoperiod (NP) or a regime of two 6-mo seasonally accelerated light increases and decreases (2CP). The T_3 and T_4 values were related to data on nutritional state, growth, and reproductive status, obtained in this study or previously (Johnston et al. 1990). Of particular interest was the influence of the photocycle on plasma TH levels in maturing female salmon. In one of the few experimental studies conducted to date on teleost thyroid cycles, Cyr et al. (1988a) showed for rainbow trout (*Oncorhynchus mykiss*) held at a constant temperature and on a constant food ration that the seasonal profiles of both female reproductive status and plasma TH levels where shifted to approximately the same extent by photoperiod manipulation. However, it was unclear if the seasonal changes in plasma TH levels represented independent responses to photoperiod or whether they were secondary to photoperiodically regulated changes in female reproductive status.

Materials and Methods

In December 1986, 46 postspawned female and 30 male Atlantic salmon (Miramichi River stock) were captured in a trap on the Morell River, Prince Edward Island. They were anesthetized (MS222, 0.1 g/L), tagged, weighed, measured (fork length), and assigned randomly to one of two 3-m-diameter center-draining tanks (see Johnston et al. 1990 for further details on the holding conditions and diet. Each tank received Cardigan River (Prince Edward Island) water (0.38 L/min) which varied from approximately 0 to 15°C seasonally (Fig. 1). On December 21, one tank was exposed to NP and the other to 2CP (Fig. 1). Commencing in January 1987, salmon were force-fed freshly thawed and vitamin-fortified silversides (*Menidia menidia*), immature smelts (*Osmerus mordax*), mature smelts, or immature capelin (*Mallotus villosus*). Feeding began slowly in February. By April, a strong feeding response had developed and force-feeding was not required. Prior to sampling, salmon were starved for 24 h and then weighed, measured, and bled from caudal vessels using a heparinized syringe. The resulting plasma was frozen at −20°C. The fish were returned to their tank except for some females which were sacrificed at intervals to assess ovarian development.

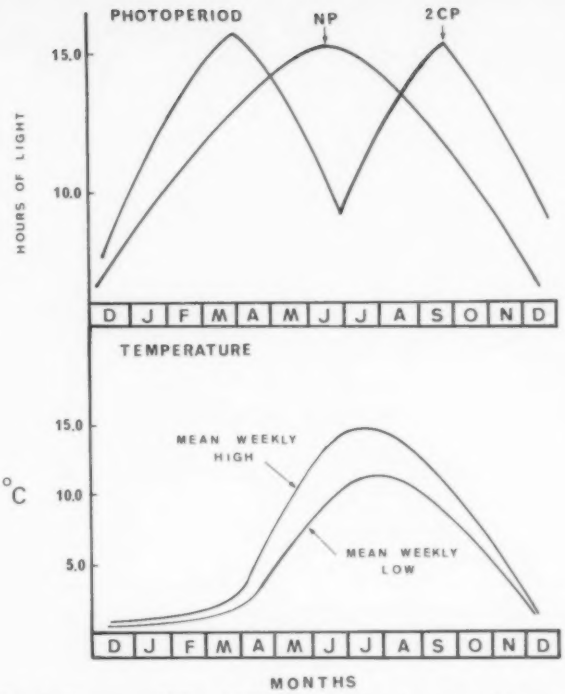

FIG. 1. Summary of NP and 2CP photocycles and mean weekly water temperatures supplied to each experimental regime (reproduced from Johnston et al. 1990).

Virgin wild salmon (10 male and 10 female) were trapped as they ascended the Morell river in July and August 1987. They were held in the laboratory under the NP photocycle.

Plasma hormone levels were measured by radioimmunoassay for T_4 and T_3 (Cyr et al. 1988a) and E_2 (Cyr and Eales 1988a). The number of plasma samples analyzed at each time interval is shown in Table 1.

The influences of the main variables (season, photocycle, and gender) on plasma T_4, T_3, or T_4/T_3 ratio were determined using the General Linear Model (SAS Institute). On all graphs, two standards errors are shown on either side of the mean.

Results

NP Regimen

Nine female (of a total of 23) and four male (of a total of 15) kelts were killed for gonadal measurements or died during the study. Of the surviving females, 56% spawned (released eggs) between 7 and 19 November; the remaining females did not mature. All of the surviving males attained spawning status (milt release) by late September.

Regardless of gender or eventual reproductive state, plasma T_4 rose to a peak at the beginning of April and then reverted to sustained lower summer levels, which were particularly low in nonfeeding individuals (Fig. 2). Plasma T_4 had risen for all groups by September. Plama T_3 attained peak values at the beginning of April and maintained generally high values until August (Fig. 3). However, in early July, plasma T_3 showed a

TABLE 1. Number of plasma samples analyzed for T_4 and T_3 (and E_2 in parentheses) for each regimen from February to December 1987. S = spawning, M = male, NP = natural photoperiod, NS = nonspawning, F = female, 2CP = two-cycle photoperiod. Fish that did not feed were not included.

	Feb.	Apr.	May	July	Aug.	Sept.	Oct.	Nov.	Dec.
S F NP	6 (—)	6 (5)	4 (—)	7 (7)	7 (7)	— (—)	— (6)	— (8)	4 (6)
NS F NP	13(—)	12 (7)	12 (—)	10 (4)	7 (8)	8 (7)	— (—)	— (—)	8 (7)
NS F 2CP	21 (—)	23 (18)	19 (—)	17 (12)	20 (—)	21 (19)	— (—)	— (18)	17 (16)
S M NP	10 (—)	12 (3)	12 (—)	6 (2)	11 (6)	8 (5)	— (—)	— (—)	10 (9)
S M 2CP	14 (—)	13 (—)	9 (—)	8 (—)	7 (—)	6 (4)	— (—)	— (—)	6 (4)
NS M 2CP	— (—)	— (6)	— (—)	— (7)	4 (—)	6 (5)	— (—)	— (11)	4 (7)
Wild male grilse	— (—)	— (—)	— (—)	8 (—)	9 (7)	6 (10)	— (—)	— (—)	— (—)
Wild female grilse	— (—)	— (—)	— (—)	10 (—)	8 (7)	10 (7)	— (—)	— (—)	— (—)

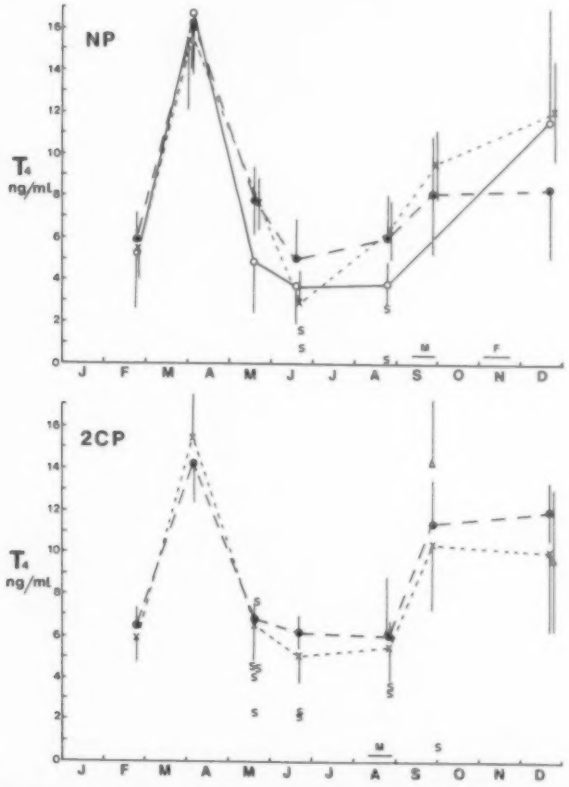

FIG. 2. Seasonal changes in plasma T_4 for salmon held under NP or 2CP photocycles. O, reproducing females; ●, nonreproducing females; ×, reproducing males; △, nonreproducing males; S, individual fish that did not feed. Each point represents the mean ± 2 SEM of 4–23 individuals. Details of samples sizes are provided in Table 1. F and M indicate the attainment of spawning status by females and males, respectively. There was a significant effect of season ($p < 0.0001$) but no effect of photocycle or gender on plasma T_4.

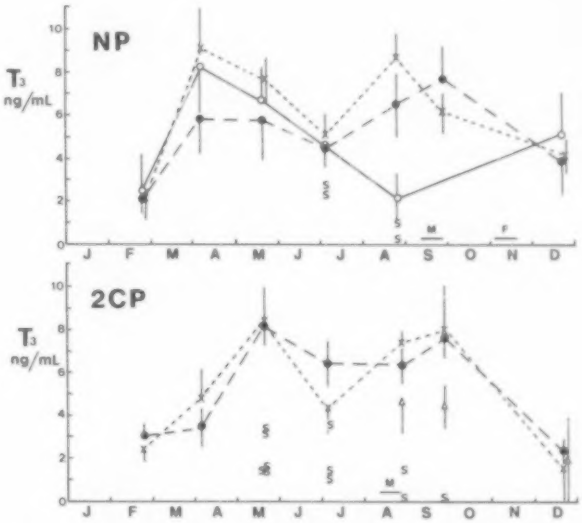

FIG. 3. Seasonal changes in plasma T_3 for salmon held under NP or 2CP photocycles (see legend to Fig. 2 for key to symbols and further details). There was a significant effect of season ($p < 0.0001$) and photocycle ($p < 0.043$) but no effect of gender on plasma T_3.

small but consistent depression. Plasma T_3 levels were low in winter for all groups and were particularly low in nonfeeding fish. In August, plasma T_3 levels were significantly ($p < 0.0007$) lower in maturing than in nonmaturing females. The plasma T_4/T_3 molar ratio (Fig. 4) revealed a sustained trough from mid-May until late September, with the exception of the maturing females for which mean values were approximately fourfold greater than for nonmaturing females or males. T_4/T_3 ratios were also high in nonfeeding fish.

Mean plasma E_2 levels were low (<10 ng/mL) at all sampling times for male and nonmaturing female kelts (Fig. 5). For maturing females, a surge in plasma E_2 occurred in late August.

2CP Regime

Two female (of a total of 23) and three male (of a total of 15) kelts were killed for gonadal measurements or died. None of the surviving females attained spawning status during the study period, but all females eventually matured and released eggs by June of the following year (1988). Of the surviving males, 77% attained spawning status in late August, 1 mo before that of NP fish.

In both males and females, plasma T_4 rose to a peak in April and then reverted to lower summer values, which were particularly low in nonfeeding individuals (Fig. 2). Plasma T_4 was high in all groups in September and December. In all respects the plasma T_4 profiles were similar for the NP and 2CP regimes. In both males and females, plasma T_3 reached a peak in late May, and not at the beginning of April as observed for the NP fish (Fig. 3). However, as in the NP regimen, plasma T_3 was high from May through to September with a small but consist-

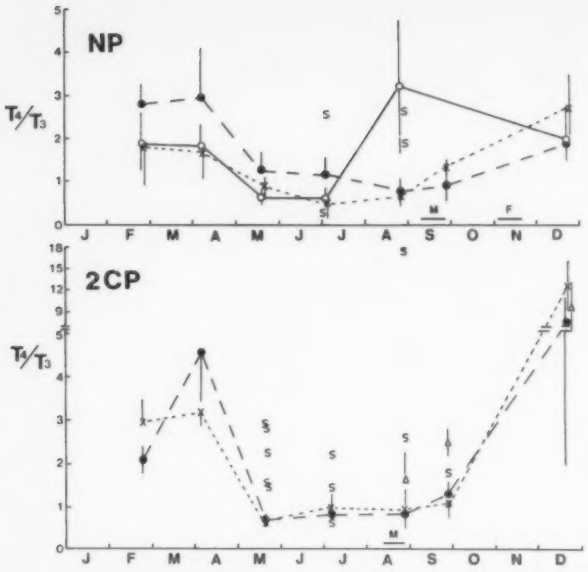

FIG. 4. Seasonal changes in plasma T_4/T_3 ratio for salmon held under NP or 2CP photocycles (see legend to Fig. 2 for key to symbols and further details). There was a significant effect of season ($p < 0.0001$) and photocycle ($p < 0.040$) but no effect of gender on plasma T_4/T_3.

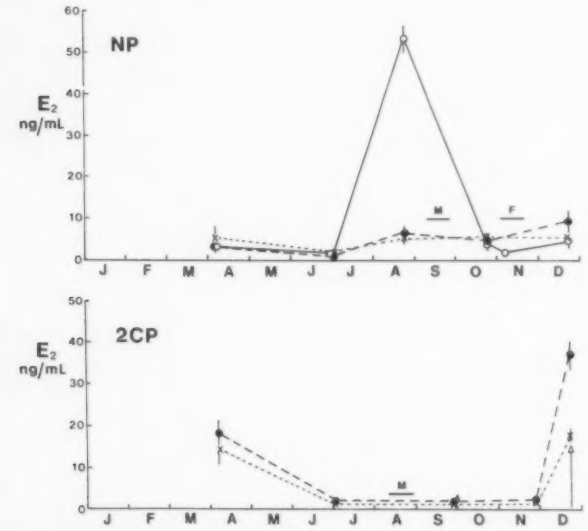

FIG. 5. Seasonal changes in plasma E_2 for salmon held under NP or 2CP photocycles (see legend to Fig. 2 for key to symbols and further details).

ent depression in early July. The plasma T_4/T_3 ratio for the 2CP fish exhibited a more extreme seasonal profile than that for the NP fish (Fig. 4). In December the T_4/T_3 ratio of the 2CP fish exceeded fourfold that of the NP fish. The ratio was particularly low from May to late September.

Plasma E_2 was low in both males and females from early July to late November, with higher values in early April and December (Fig. 5). The December surge in plasma E_2 was associated with ovarian development (Johnston et al. 1990).

TABLE 2. Mean plasma levels (SEM) of TH of Atlantic salmon captured during their first upstream spawning migration in July and August and then held in the laboratory under seasonal temperature and photoperiod (NP). M = male, F = female, n = 6–10.

Date	Sex	T_3 (ng/mL)	T_4 (ng/mL)	T_4/T_3 (molar ratio)	E_2 (ng/mL)
July 9	F	6.4	9.8	1.4	—
		(1.1)	(1.8)	(0.2)	
	M	7.7	7.1	0.8	—
		(0.8)	(1.2)	(0.1)	
Aug. 31	F	2.7	6.9	2.4	58
		(0.4)	(0.5)	(1.0)	(10)
	M	7.5	6.4	0.7	9
		(0.8)	(1.0)	(0.1)	(2)
Sept. 27	F	0.6	7.5	12.4	33
		(0.2)	(0.8)	(1.1)	(3)
	M	3.5	8.0	2.0	0.8
		(0.2)	(0.5)	(0.2)	(1.8)

Wild-Caught Fish

All surviving females (one died) attained spawning status in late October; all males (no mortality) attained spawning status in late September or early October.

From early July until late September, mean plasma T_4 levels remained between 6.4 and 9.8 ng/mL and did not differ between sexes (Table 2). Over this period, plasma T_3 fell and T_4/T_3 rose in both males and females but the decrease was particularly marked in females. Plasma E_2 levels were high in females in August and September.

Growth, Rematuration, and Blood Chemistry

Additional data relating to seasonal changes in body weight, condition factor, mortality, ovarian weight, oocyte diameter, and plasma alkaline phosphatase, calcium, cholesterol, and triglyceride levels are provided in Johnston et al. (1990).

Discussion

Circulating thyroid hormone levels of both male and female reconditioned Atlantic salmon kelts held in captivity in freshwater at seasonal temperatures and under a simulated natural photoperiod showed marked seasonal profiles. Changes were particularly clear-cut for T_4, with a major peak in early April and an upswing in September. Plasma T_3 levels also showed spring and fall elevations, but they were less pronounced than those for T_4 with which they did not necessarily coincide. This asynchrony in plasma T_4 and T_3 levels created a marked seasonal change in the plasma T_4/T_3 ratio. This ratio cannot be unambiguously interpreted from the physiological standpoint without knowledge of T_3 and T_4 production/clearance rates. However, it is useful as a nonspecific indicator of altered thyroid function.

The T_4 seasonal profile was extremely robust, being refractory to gender, eventual reproductive state, or imposition of a 2CP photocycle. Based on the limited data available in this study, parallel changes in plasma T_4 occurred in wild-caught salmon spawning for the first time. In female rainbow trout, an inverse relationship was demonstrated between ovarian vitellogenic development and circulating T_4 under several photocycle regimes (Cyr et al. 1988a). That correlative study suggested a possible influence of reproductive state on plasma T_4.

Clearly in postspawned Atlantic salmon the plasma T_4 level is not determined by the state of female gonad development, and for this species, and possibly the rainbow trout and other salmonids, alternative explanations of the T_4 seasonal cycle must be entertained.

Plasma T_4 levels were unaffected by the 2CP regimen, indicating no response to this particular photocycle. This appears to differ from the situation in rainbow trout where photocycle manipulation modified the seasonal T_4 cycle (Cyr et al. 1988a). However, in the present study, photoperiod was increasing during the first three calendar months under both NP and 2CP regime, and this, in conjunction with the common preceding decreasing photoperiod (Duston and Bromage 1986, 1987), may have been sufficient to set the T_4 profile for the 12-mo duration of the present study.

The plasma T_3 profile was also robust and parallel in males and nonreproducing females. However, in vitellogenic NP females and wild-caught females approaching reproduction (Johnston et al. 1990), plasma T_3 was very low, implying reduced T_3 generation and/or increased plasma T_3 clearance. These data are consistent with the observations of Cyr et al. (1988a) for rainbow trout in which the plasma T_3 level decreased when plasma E_2 attained high levels during vitellogenesis and support the findings of Cyr et al. (1988b) that E_2 administration to rainbow trout reduces the V_{max} (functional level) of the hepatic T_4 5′-monodeiodinase which generates T_3 from T_4. Thus in contrast with T_4, the T_3 plasma level does seem to be governed by female reproductive status. As suggested previously (Cyr et al. 1988a), the low plasma T_3 levels may suppress somatic growth when energy is being channelled into egg development.

The plasma T_3 profile was modified by the 2CP regime in April and December, again demonstrating the lack of linkage between the level of plasma T_3 and the level of its immediate precursor, T_4. The mechanism of mediation of the change in plasma T_3 due to photocycle cannot be determined from the present experimental design. However, growth hormone (GH) is a potent stimulator of in vivo T_4 to T_3 conversion (DeLuze and Leloup 1984) and elevates the functional level of the hepatic 5′-monodeiodinase (MacLatchy and Eales 1989). Seasonal changes in GH level, as reported in goldfish (*Carassius auratus*) (Marchant and Peter 1986), could influence T_3 production and hence the plasma T_3 level.

Seasonal changes in water temperature may have influenced the plasma T_4 level. Plasma T_4 was depressed during the summer when temperatures were highest. This is consistent with the inverse relationship found in rainbow trout between plasma T_4 and acclimation temperature (Eales et al. 1982). However, the pronounced spring surge in plasma T_4 occurred when water temperaures were low (approximately 1°C) and slowly increasing. It is unlikely, therefore, that this phase of the seasonal profile in plasma T_4 was influenced substantially by temperature. Plasma T_3 levels were generally highest during the warm summer months. However, in early July, plasma T_3 level fell consistently in both NP and CP regimes, coinciding with the highest summer temperatures. Plasma T_3 level in the rainbow trout has been shown to be uninfluenced by acclimation temperature, although T_3 plasma clearance is increased (Eales et al. 1986) and T_3 binding to plasma proteins is decreased (Eales and Shostak 1986).

Plasma TH levels in salmonids are also modified by food intake (Milne et al. 1979; Flood and Eales 1983; Eales 1988). In February, most fish were feeding but food intake was low; however, a strong feeding response had developed by April, and nutrient intake may have contributed to the T_4 surge at that time. An effect of feeding on plasma TH is supported by the lower values for both T_4 and T_3 for nonfeeding fish.

As described by Johnston et al. (1990), the Atlantic salmon used in this study approximately doubled their weight between early April and late August. This period of growth coincided with the lowest T_4 levels, the highest T_3 levels, and the lowest T_4/T_3 ratios, lending correlative support to the generally accepted view that TH, and in particular T_3, exert a role in promoting somatic growth in salmonids (Higgs et al. 1982).

The present seasonal profiles resemble those described recently by Dickhoff et al. (1989) who held previously unspawned 4- or 5-yr-old Atlantic salmon in sea cages and transferred them to freshwater just prior to November spawning. The seasonal ranges of both T_4 (>20 to <5 ng/mL) and T_3 (>8 to <1 ng/mL) were comparable between Dickhoff's study and ours despite major differences in salinity, temperature, prior metabolic state, and previous reproductive history. Furthermore, there were similarities in seasonal trends. In both studies, T_4 decreased in spring or early summer and increased again in fall, with no significant difference between males and females. Plasma T_3 increased from February onwards but showed a decrease in July. In the case of males and nonspawning females, this decrease was temporary, but in spawning females, T_3 continued to fall as egg maturation proceeded. In combination, these two studies emphasize the robustness, and seemingly tight endogenous control, of the TH seasonal cycles in adults of this species despite differences in major environmental factors and prior reproductive experience.

There is mounting evidence that T_3, the presumed cellularly active form of TH in fish, acts in a permissive capacity to facilitate gonadotropin stimulation of teleost oocyte development (Hurlburt 1977; Dettlaff and Davydova 1979; Epler and Bieniarz 1983; Sen and Bhattacharya 1981; Cyr and Eales 1988a, 1988b) and also oocyte final maturation (Pickering and Christie 1981; Sullivan et al. 1989; Dickhoff et al. 1989; Norberg et al. 1989). The present T_3 profiles are consistent with such roles in the Atlantic salmon kelts. In nonspawning NP females in spring, plasma T_3 was lower, and the T_4/T_3 ratio higher, than that for the NP females which eventually spawned. Furthermore, under the 2CP regimen, in contrast with the NP regimen, the plasma T_3 in the nonreproducing females was low in April and did not reach high levels until May. It is possible that the T_3 levels during a critical window in spring were below the threshold to permit gonadotropin stimulation of oocyte development and subsequent reproduction. Plasma T_3 levels were low in NP females prior to spawning but such levels may be adequate to facilitate gonadotropin-induced ovarian maturation as postulated by Dickhoff et al. (1989). Insufficient sampling points were available to determine T_3 levels at the actual time of oocyte maturation. Levels of TH and particularly T_3 may rise at that time (Pickering and Christie 1981; Norberg et al. 1989). No differences in plasma T_4 were seen between reproducing and nonreproducing fish, underlining the importance of plasma T_3 rather than plasma T_4 in regulating early reproductive development in the female.

We conclude that circulating T_4 and T_3 levels in postspawned Atlantic salmon undergoing reconditioning in captivity in freshwater are determined by different factors resulting in asynchronous and seemingly independent seasonal profiles. Furthermore, these seasonal cycles resemble those described by Dickhoff et al. (1989) for Atlantic salmon spawning for the

first time. The extremely robust T_4 profile was not influenced by gender or eventual reproductive state or the particular imposed photocycle, and its general inflexibility implies a lack of fine control which may be appropriate for a precursor or prohormone molecule. The presumed active TH, T_3, also exhibits a seasonal profile but one that appears to be modulated to a greater degree by female reproductive state, nutrient intake, and photocycle. Furthermore, T_3 levels in April may have some role to play in determining the eventual gonad maturation in the female. The above observations should be of value in the design of experiments to determine the role of T_3 in the reconditioning and maturation of Atlantic salmon kelts and the possible practical use of T_3-supplemented diets to enhance kelt reconditioning and reproductive success.

Acknowledgements

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Biological and Environmental Control of Mercury Accumulation by Fish in Lakes and Reservoirs of Northern Manitoba, Canada

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Jackson, T. A. 1991. Biological and environmental control of mercury accumulation by fish in lakes and reservoirs of northern Manitoba, Canada. Can. J. Fish. Aquat. Sci. 48: 2449–2470.

Enlargement of northern Manitoba lakes to form hydroelectric reservoirs caused a rise in the Hg content of walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*), yellow perch (*Perca flavescens*), and spottail shiner (*Notropis hudsonius*) owing to stimulation of Hg methylating microbes by submerged terrestrial organic matter. However, an increase in the supply of organic substrates beyond a critical amount mitigated this effect, apparently by promoting Hg demethylation and production of Hg-binding agents such as sulfides. Fish species, even at the same trophic level, differed markedly in their Hg content, Hg – fork length relationships, and regional and temporal variations in Hg content; this is ascribed to differences in habitat preference, metabolic rate, age, growth rate, size, biomass, diet, and excretory pathways, and hence different responses and degrees of exposure to spatially varying conditions influencing Hg speciation and availability. Whitefish had an anomalously weak tendency to accumulate CH_3Hg^+ and a high ratio of liver CH_3Hg^+ to muscle CH_3Hg^+, suggesting a special mechanism of excretion. Only walleye Hg correlated significantly with CH_3Hg^+ production in offshore mud, indicating the value of walleye for whole-lake Hg bioassays and the validity and utility of the methods used to quantify CH_3Hg^+ production.

L'agrandissement de certains lacs du nord du Manitoba pour les transformer en réservoirs hydroélectriques a provoqué une augmentation de la teneur en Hg dans le doré (*Stizostedion vitreum*), le grand brochet (*Esox lucius*), le grand corrégone (*Coregonus clupeaformis*), la perchaude (*Perca flavescens*) et la queue à tache noire (*Notropis hudsonius*). Cette augmentation est due à la stimulation de la croissance de microorganismes capables de méthyler le Hg par la présence de matières organiques terrestres submergées. Cependant, un apport de matières organiques supérieur à une certaine quantité critique atténue cet effet en favorisant apparemment la déméthylation du Hg et la production de ligands du Hg tels les sulfures. La teneur en mercure, la relation Hg – longueur à la fourche et les variations régionales et temporelles de cette teneur ont fluctué beaucoup d'une espèce à l'autre, qu'elles appartiennent ou non au même niveau trophique. Ces fluctuations sont attribuables aux différences d'habitat, de taux métabolique, d'âge, de taux de croissance, de taille, de biomasse, de régime alimentaire et de voies d'excrétion, d'où découlent des réactions et des degrés d'exposition divers à des conditions, variables dans l'espace, qui agissent sur la spéciation et la disponibilité du Hg. Le grand corrégone a montré une tendance anormalement faible à accumuler le CH_3Hg^+ et a présenté un rapport CH_3Hg^+ hépatique/CH_3Hg^+ musculaire élevé, ce qui laisse croire à un mécanisme d'excrétion particulier. Une corrélation significative entre la production de CH_3Hg^+ dans les boues du large et la teneur en mercure de l'organisme n'a été observée que chez le doré, ce qui montre la valeur du doré pour le dosage biologique du Hg à l'échelle d'un lac ainsi que la validité et l'utilité des méthodes employées pour quantifier la production de CH_3Hg^+.

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In northern Manitoba (Canada), enlargement of riverine lakes to form reservoirs caused a marked increase in the concentrations of mercury (Hg) in fish inhabiting these lakes (Bodaly and Hecky 1979; McGregor 1980; Bodaly et al. 1984, 1987a, 1987b, Derksen and Green 1987). The Hg problem was one of several adverse effects of the Churchill River diversion, a controversial hydroelectric project which involved impoundment and rerouting of Churchill River water, resulting in the raising of lake levels and flooding of adjacent land in 1976. In lakes transformed into reservoirs, a sharp rise in the Hg content of several fish species began within 2 yr following the onset of flooding, and the mean Hg concentrations in walleye and northern pike muscle rose above the 0.5 μg/g limit imposed by the Federal Food and Drug Directorate on fish marketed in Canada for human consumption. However, fish inhabiting lakes unaffected by hydroelectric development remained at background levels. The Hg in both the reservoirs and the unaltered lakes was derived solely from diffuse, low-level background sources, there being no known point sources of Hg contamination in the region (Bodaly et al. 1984, 1987a, 1987b; Rannie and Punter 1987; Jackson 1988b).

The Hg problem resulted primarily from stimulation of the growth and activity of Hg methylating microorganisms by terrestrial organic matter (mostly remains of dead plants) in the zone of recently inundated forest- and muskeg-covered land (Bodaly et al. 1984, 1987a; Hecky et al. 1987a, 1987b, 1987c; Jackson 1987, 1988b; Ramlal et al. 1987; Ramsey and Ramlal 1987a, 1987b; Rannie and Punter 1987). The appearance of abnormally high Hg concentrations in fish following alteration of their habitat by the creation of reservoirs has been reported

repeatedly in widely separated, environmentally diverse regions of the world, indicating that the phenomenon is a common — perhaps universal — consequence of impoundment, although the causes of the problem have been most intensively studied in northern Manitoba (Bodaly et al. 1984; Jackson 1988b).

Previous papers have treated different aspects of the biogeochemistry of methyl Hg (CH_3Hg^+) and inorganic Hg in sediments and water (Jackson 1987, 1988b, 1989b), as well as the accumulation of Hg by plankton and benthic invertebrates (Jackson 1988a), in several northern Manitoba lakes representing a range of lacustrine conditions and different degrees of alteration by the Churchill River diversion. The present paper examines effects of environmental and biological processes on the accumulation of Hg by different species of fish in these lakes, with particular attention to possible causes of interspecific variations.

Field Sites, Materials, and Methods

Descriptions of the field sites and reports of work performed on sediments, water, plankton, and benthic invertebrates from these sites have been presented by Jackson (1987, 1988a, 1988b); some of the data used in the present paper were taken from these earlier publications. The sampling sites represent two "control" or "reference" lakes (Granville Lake and East Mynarski Lake) which have not been affected by the Churchill River diversion together with several lakes (comprising Southern Indian Lake and lakes of the Notigi Reservoir complex) which have been altered to a greater or lesser extent by the impoundment and rerouting of river water (Jackson 1988b, fig. 1). The samples were collected in June and August 1981 and August 1983.

The fish species included in this study are walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*), yellow perch (*Perca flavescens*), and spottail shiner (*Notropis hudsonius*). The mean Hg concentrations in muscle tissue and mean fork lengths of fish caught at the field sites during different years, as well as paired CH_3Hg^+ and total Hg data for muscle and liver, were gleaned from Bodaly et al. (1984, 1987b) and from unpublished archives of the Inspection Services Branch, Department of Fisheries and Oceans (Government of Canada), Winnipeg, Manitoba (G. W. G. McGregor, pers. comm.). The walleye, pike, and whitefish data for Southern Indian Lake represent the years 1969–82, thus permitting comparison of Hg levels before and after the year of impoundment (1976). Particular attention was devoted to samples collected from different lakes in 1980 and 1981, as these show the full range of effects due to the Churchill River diversion. The shiner and perch samples were collected in 1981 and 1982.

Total Hg in fish tissue was determined by the methods of Hendzel and Jamieson (1976). CH_3Hg^+ (more precisely, "total organic Hg") was determined by a method developed by A. Rieger of the Freshwater Institute, Winnipeg, Manitoba (pers. comm.): CH_3Hg^+ was extracted with $CuSO_4$ and NaBr (Uthe et al. 1972), taken up in methylene chloride, and then determined as elemental Hg using methods described by Hendzel and Jamieson (1976) (also see Jackson 1988b). This organic Hg fraction presumably consisted entirely, or almost entirely, of CH_3Hg^+ and is referred to as such in this paper because other organic Hg compounds have hardly ever been detected in fish (Huckabee et al. 1979; A. Rieger, pers. comm.).

Relationships between covariant sets of data were subjected to regression analysis. Correlation coefficients (r) and significance probabilities (P) were computed for linear, log-log, semi-log, parabolic, and hyperbolic regression lines, and the regression formulas yielding the highest r and P values were selected as the nearest approximations of the trends; P values ≤ 0.05 are defined as "significant."

Results and Discussion

Relationship between the Hg Content and Fork Length of the Fish

Hg levels in fish generally tend to rise with an increase in the age, and therefore the *size*, of the fish owing to accumulation of CH_3Hg^+ with increasing time of exposure (Johnels et al. 1967; Bache et al. 1971; Jernelöv and Lann 1971; Gavis and Ferguson 1972; Scott and Armstrong 1972; de Freitas et al. 1974, 1977; Scott 1974; Ruohtula and Miettinen 1975; Huckabee et al. 1979; Windom and Kendall 1979). Consequently, it was necessary, at the outset, to examine the relationships between the Hg concentrations and fork lengths of the fish and to ascertain whether the Hg data should be corrected by normalisation with respect to fork length. Another question that had to be resolved was whether it was more appropriate to relate the Hg data to fork length or to body weight. As CH_3Hg^+ concentrations and accumulation kinetics have been shown to vary as functions of weight (de Freitas and Hart 1975; Norstrom et al. 1976), it might be argued that weight is the more suitable parameter. However, this does not necessarily follow. In a study of several species from many lakes in Manitoba and northwestern Ontario, Scott and Armstrong (1972) showed that length and weight gave comparable results (not surprisingly, as the two parameters are correlated), but the authors considered length more reliable because this parameter is less prone to major short-term fluctuations (weight being strongly influenced by feeding). Furthermore, Scott (1974) reported that two different studies revealed consistent correlation between Hg and length but gave contradictory relationships between Hg and condition, which is a function of weight. In a study of fish in northern Manitoba, Derksen and Green (1987) found that Hg in walleye and pike correlated more significantly with length than with weight, although the reverse was true of whitefish. All things considered, fork length was judged to be suitable and probably preferable. In any case, practical necessity dictated the choice of fork length, as weight data were not available for all sample sets. Age might be the most useful parameter of all, at least for some species (Derksen and Green 1987), but since direct measurements of age were not available, fork length had to do duty for the approximation of age.

None of the fish species gave a significant correlation between the mean Hg concentrations and corresponding mean fork lengths recorded for the different field sites, with the exception of walleye in lakes affected by impoundment (Tables 1 and 2). Moreover, two of the five species unexpectedly showed *negative* correlations. Relationships between Hg concentrations and environmental variables (see below) did not change appreciably when the Hg data were normalised with respect to fork length, even in the case of walleye. Thus, there was no need to recalculate the raw Hg data to take variation with size into account.

Other workers, too, have reported poor correlations between Hg content and body size in fish from lakes along the Churchill

TABLE 1. Mean Hg concentrations (nmol/g fresh weight) in muscle tissue and mean fork lengths northern Manitoba lakes in the years 1980, 1981, and 1982. n.d. = no data; — = not applica pers. comm.).

	Shiner				Perch					
	1981		1982		1981		1982		1980	
Sampling site	Hg	Length	Hg	Length	Hg	Length	Hg	Length	Hg	Len
Granville Lake	0.3	4.22	0.2	7.42	0.1	6.60	0.1	7.11	n.d.	n.
East Mynarski Lake	0.40	5.43	0.25	7.08	0.1	4.60	0.1	7.48	n.d.	n.
Southern Indian Lake										
Long Bay[a] (main basin)	0.3	4.72	0.50	8.12	n.d.	n.d.	n.d.	n.d.	n.d.	n
South Bay	0.65	5.15	0.50	7.27	n.d.	n.d.	n.d.	n.d.	1.0	3
Methyl Bay (offshore)	n.d.	n.d.	0.55	7.12	n.d.	n.d.	0.3	6.25	n.d.	n
Notigi Reservoir										
Rat Lake	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	1.6	4
West Mynarski Lake	0.70	8.16	0.75	7.46	0.3	5.35	0.55	6.55	n.d.	n
Central Mynarski Lake	0.65	7.90	n.d.	n.d.	0.4	5.58	n.d.	n.d.	n.d.	n
West or Central Mynarski Lake (exact location unknown)	—	—	—	—	—	—	—	—	1.2	4
Notigi Lake (west basin)	0.90	3.06	0.95	7.51	n.d.	n.d.	0.90	6.57	n.d.	n
Notigi Lake (east basin)	0.95	2.90	1.2	7.62	n.d.	n.d.	n.d.	n.d.	n.d.	n
Notigi Lake (basin not recorded)	—	—	—	—	—	—	—	—	0.6	4

[a]Now called Wupaw Bay.

lengths (cm) of spottail shiner, yellow perch, lake whitefish, walleye, and northern pike in applicable. Sources of data: Bodaly et al. (1984, 1987b); G. W. G. McGregor (unpubl. data;

Whitefish				Walleye				Pike			
1980		1981		1980		1981		1980		1981	
Hg	Length	Hg	Length	Hg	Length	Hg	Length	Hg	Length	Hg	Length
.d.	n.d.	n.d.	n.d.	n.d.	n.d.	1.2	45.5	n.d.	n.d.	1.9	71.1
.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
.d.	n.d.	0.65	31.25	n.d.	n.d.	2.0	37.0	n.d.	n.d.	n.d.	n.d.
.0	33.3	0.70	32.7	2.9	37.6	3.2	38.0	3.9	53.7	4.4	55.4
.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
.6	42.2	n.d.	n.d.	5.73	40.8	n.d.	n.d.	11.6	n.d.	n.d.	n.d.
.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
.2	46.3	n.d.	n.d.	8.82	41.9	n.d.	n.d.	6.68	60.2	n.d.	n.d.
.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
0.6	42.1	1.1	30.9	13.7	45.2	9.37	41.6	9.72	78.8	8.47	58.1

TABLE 2. Correlation matrix relating the Hg content of spottail shiner, yellow perch, lake whitefish, walleye, and northern pike muscle to the fork lengths of the fish. The data employed for the regression analyses were the mean values for the years indicated. r = correlation coefficient; P = significance probability.

	r	P
Shiner (1981 and 1982)	−0.109	>>0.1
Perch (1981 and 1982)	−0.217	>>0.1
Whitefish (1980 and 1981)	0.452	>>0.1
Walleye (1980 and 1981)	0.578[a]	>0.1[a]
Pike (1980 and 1981)	0.456	>>0.1

[a]If Granville Lake data are omitted, $r = 0.986$ and $P < 0.001$. Thus, for *reservoir* data, the correlation is highly significant.

River diversion route (McGregor 1980; Bodaly et al. 1984). Derksen and Green (1987) noted a tendency for Hg concentration to increase with size and age among walleye, pike, and whitefish (although occasional inverse relationships occurred); but the significance probabilities of the correlations were not given, and, judging from the authors' plots of Hg content against fork length, many of the relationships are probably not significant.

Although the correlations between Hg content and fork length (Table 2) are generally weak, they reflect known differences in the characteristics of the species as represented by the samples analysed, indicating that they may be a source of useful information on interspecific variations in the kinetics of Hg bioaccumulation. Walleye, pike, and whitefish, the three species with the largest body sizes, the longest life spans, and (judging from their size ranges and corresponding approximate ages) the lowest rates of growth and metabolism (Scott and Crossman 1973; Lagler et al. 1977), gave *positive* correlations, as expected, between Hg and length and yielded the highest correlation coefficients; but shiner and perch, the two species with the smallest body sizes, the shortest life spans, and (presumably) the highest rates of growth and metabolism (Scott and Crossman 1973; Lagler et al. 1977), gave *inverse* correlations and much lower correlation coefficients. In accordance with generally accepted concepts of Hg bioaccumulation, we may conclude, on the one hand, that the older, larger individuals in the walleye, pike, and whitefish populations tended to have larger accumulations of Hg because they had undergone longer exposure to environmental CH_3Hg^+, which is taken up more rapidly than it is excreted (Huckabee et al. 1979); owing to their low growth rates and large body sizes, growth dilution of CH_3Hg^+ and clearance of CH_3Hg^+ from their body tissues were not rapid enough to offset this effect (de Freitas et al. 1974, 1977; de Freitas and Hart 1975; Ruohtula and Miettinen 1975; Norstrom et al. 1976; Huckabee et al. 1979). On the other hand, the fact that increasing age and size had the opposite effect on shiner and perch probably signifies that their high growth rates resulted in growth dilution of their body burdens of CH_3Hg^+ (de Freitas et al. 1974; Huckabee et al. 1979), offsetting the tendency of their high metabolic rates to accelerate CH_3Hg^+ uptake (Reinert et al. 1974; Scott 1974; de Freitas and Hart 1975; Norstrom et al. 1976) and outweighing the effect of age-dependent bioaccumulation. Relatively rapid excretion of CH_3Hg^+ owing to small body size (de Freitas and Hart 1975; Norstrom et al. 1976) may also have been a contributing factor. Thus, the results suggest that marked interspecific differences in the kinetics of Hg accumulation arose from contrasting net effects of several biological processes operating simultaneously, although the contrast between walleye, pike, and whitefish on the one hand and shiner and perch on the other may be due to the inferred higher level of maturity of the specimens representing the former group as well as inherent differences between the species. A possible explanation for the general insignificance of the correlations between Hg and length is that the various contributing factors tended to cancel each other's effects, producing weak *net* effects. Whether selective reduction of the larger size classes of walleye, pike, and whitefish by fishing has had any effect is unknown.

Combined Effects of Biological and Environmental Factors on Hg accumulation by Different Species of Fish

Variation over time before and after flooding

Within about 2 yr after the onset of impoundment, Hg levels in walleye, pike, and whitefish in Southern Indian Lake rose abruptly, indicating a dramatic effect of flooding, but the three species differed markedly in their subsequent variations over time (from 1978 to 1982) (Fig. 1), as mentioned by Bodaly et al. (1984): walleye Hg quickly levelled off and showed no further significant changes whereas pike Hg continued to rise unabated, whilst whitefish Hg, after a brief initial upsurge, declined steeply and progressively and had returned to the range of background values by 1982. In both walleye and pike, Hg levels in the postimpoundment phase consistently exceeded 0.5 μg/g (2.5 nmol/g), but whitefish never reached this level. The highest pre- *and* postimpoundment Hg levels occurred in pike. Also note that preimpoundment Hg in both walleye and pike tended to increase gradually with time. The pre- and postimpoundment pike data alone do not constitute unequivocal evidence for an effect of flooding because they appear to indicate a progressive increase in Hg level over the entire interval 1969–82, with only the suggestion of a discontinuity due to flooding. However, the walleye and whitefish data show a sharp contrast between pre- and postimpoundment Hg levels, leaving no reasonable doubt that it was caused by flooding. For additional information on time-dependent variations, see Bodaly and Strange (1987) and Hecky et al. (1987a).

On the basis of the kinetics of Hg accumulation from 1978 to 1982 (Fig. 1) as well as the abundance of Hg in muscle tissue (Table 1), the effect of impoundment on Hg accumulation by these fish increased in the order whitefish <<walleye < pike. The difference between the results for pike and walleye may seem odd, considering that the two species occupy the same trophic level and have similar diets and feeding habits (Scott and Crossman 1973), but it can be explained by known differences in habitat preference and behaviour, which, in turn, are linked to differences in metabolic rate: the relatively sluggish pike mainly inhabit shallow inshore regions, where, in newly formed reservoirs, the rate of CH_3Hg^+ production is highest, but the more active walleye range over a wider area and are apt to venture into offshore regions, where the rate of CH_3Hg^+ production is lower (Derksen and Green 1987; Jackson 1987). In Southern Indian Lake, where the zone of submerged land is rather narrow, this behavioural difference could have caused the net rate of Hg bioaccumulation to be lower, and the levelling off of Hg concentrations to begin sooner, in walleye than in pike. The slight temporal increase in preimpoundment walleye and pike Hg probably reflects the well-known progressive global increase in the abundance of anthropogenic Hg in the atmosphere (Matheson 1977; Andren and

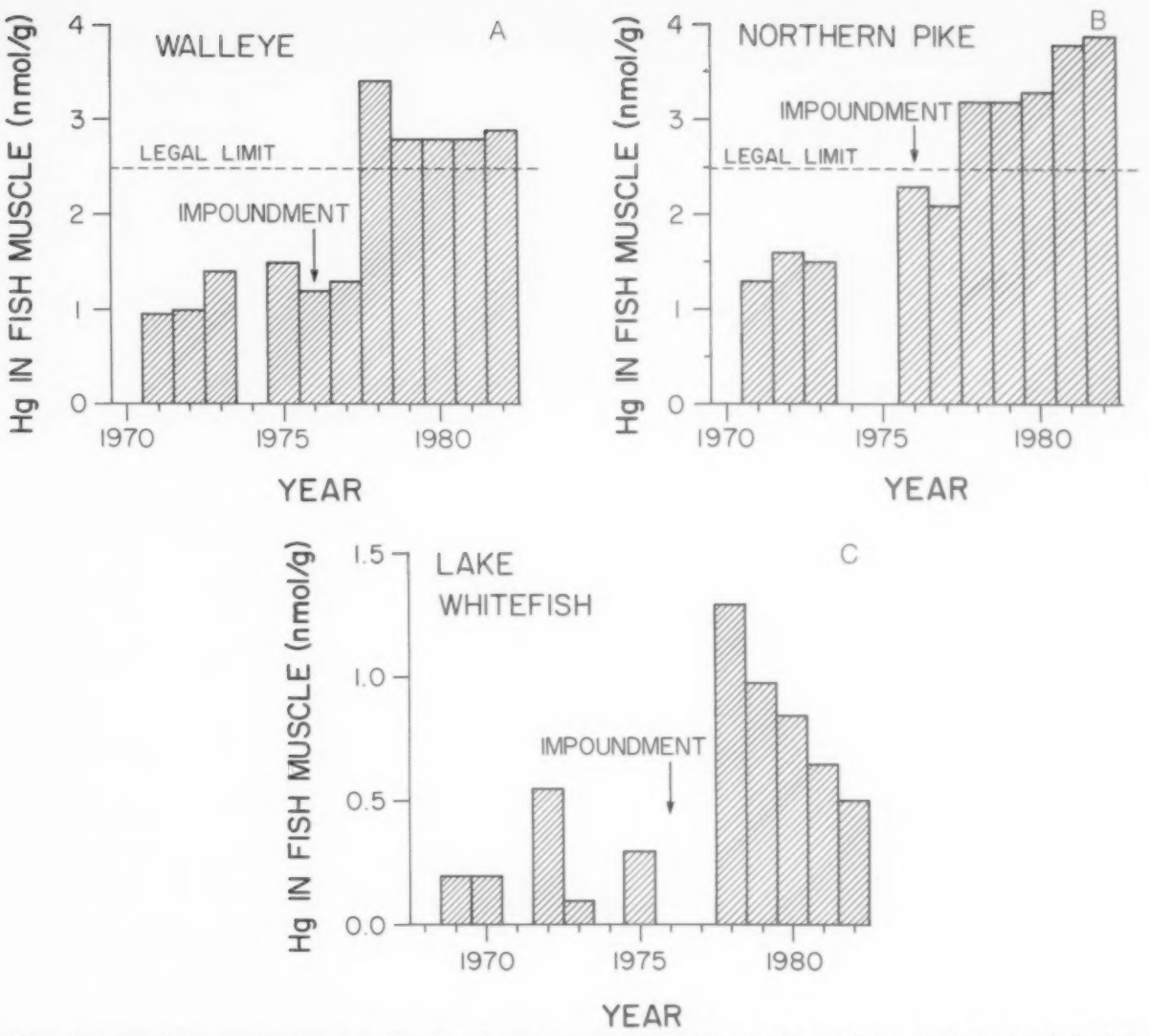

FIG. 1. Variations in the mean Hg content of (A) walleye, (B) northern pike, and (C) lake whitefish muscle over time in Southern Indian Lake. The gaps are due to absence of data, and the arrow indicates the onset of impoundment.

Nriagu 1979; Bodaly et al. 1984). The rapid temporal decrease in whitefish Hg after the initial increase suggests that the metabolic pathways of Hg in whitefish are in some way fundamentally different from those in pike and walleye. The low concentrations of Hg in whitefish may be due at least in part to the diet of this species and its lower position in the food chain, as well as its preference for deepwater environments (Scott and Crossman 1973), where rates of CH_3Hg^+ production are relatively low (Derksen and Green 1987) and where low temperatures may retard the accumulation of CH_3Hg^+ (Reinert et al. 1974); but the decrease in Hg level with time suggests a special mechanism for elimination of CH_3Hg^+ (see below).

Responses to regional variations in ambient conditions

Among all five species of fish, Hg concentrations tended to be highest in lakes where the postimpoundment rise in water level had been greatest (Fig. 2) (Bodaly et al. 1984, 1987a, 1987b; Derksen and Green 1987). Thus, the Hg content of fish from different sampling localities increased in the order "control" lakes < Southern Indian Lake sites < Notigi Reservoir lakes. The reason for this relationship is that CH_3Hg^+ production rates have been abnormally high in the regions of recently flooded land owing to stimulation of microbial activity by submerged terrestrial organic matter (Bodaly et al. 1984; Hecky et al. 1987a, 1987b, 1987c; Jackson 1987, 1988b; Ramsey and Ramlal 1987a, 1987b). The greater the rise in water level, the greater the proportion of flooded land to preimpoundment lake bottom, and therefore the higher the net rates of CH_3Hg^+ production and bioaccumulation in the lake.

Nevertheless, whitefish, again, were anomalous, as they gave an insignificant correlation ($P >> 0.1$) between Hg content and rise in water level (Fig. 2E) whereas all other species gave correlations that were significant at levels of probability ranging from 0.05 to < 0.001 (Fig. 2A–2D). The weakness

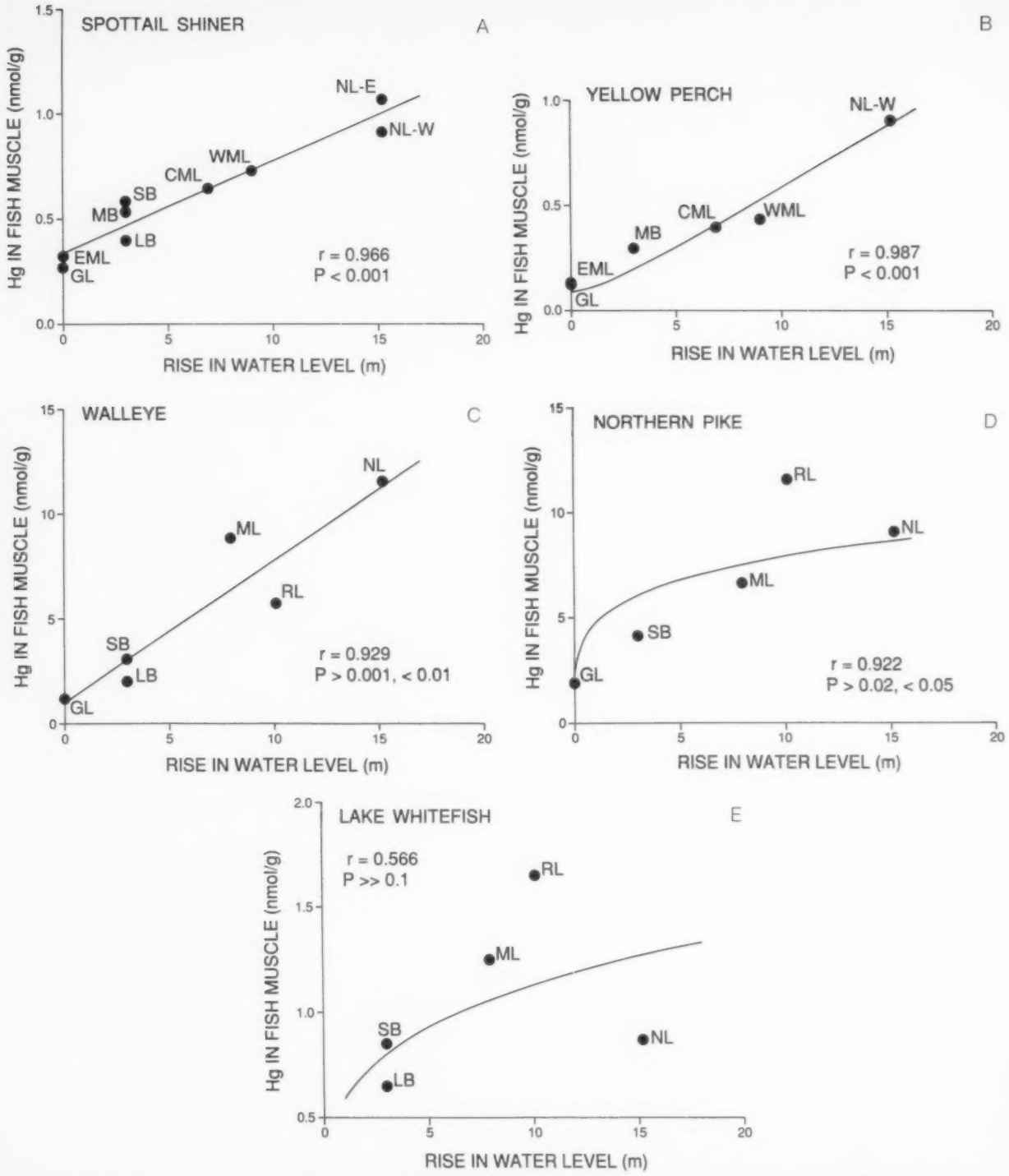

FIG. 2. Variations in the mean Hg content of (A) spottail shiner, (B) yellow perch, (C) walleye, (D) northern pike, and (E) lake whitefish muscle in different lakes as functions of the rise in water level following impoundment and diversion of the Churchill River. Dates of sample collection: walleye, pike, and whitefish, 1980 and 1981; shiner and perch, 1981 and 1982. GL = Granville Lake; EML = East Mynarski Lake; LB, SB, and MB = Long Bay, South Bay, and Methyl Bay, respectively, of Southern Indian Lake; RL = Rat Lake; WML = West Mynarski Lake; CML = Central Mynarski Lake; ML = West or Central Mynarski Lake, or both (exact locality unknown); NL-W = west basin of Notigi Lake; NL-E = east basin of Notigi Lake; NL = Notigi Lake (basin unknown).

TABLE 3. Ratios computed from total Hg and CH_3Hg^+ concentrations in muscle and liver tissue of walleye, northern pike, and lake whitefish collected from four regions of Southern Indian Lake in 1980 (courtesy of G. W. G. McGregor, unpubl. data; pers. comm.). CH_3Hg^+ was determined as Hg. N = number of samples; $\bar{X}$ = mean. For location of sampling regions, see McGregor (1980, fig. 1) or Jackson (1988b, fig. 1).

		CH_3Hg^+/total Hg											
		Muscle			Liver			Liver Hg/Muscle Hg			Liver CH_3Hg^+/ Muscle CH_3Hg^+		
Sampling region	Species	N	$\bar{X}$	Range	N	$\bar{X}$	Range	N	$\bar{X}$	Range	N	$\bar{X}$	Range
South Bay	Walleye	19	0.825	0.702–0.962	18	0.890	0.667–1.2	18	0.384	0.204–0.516	18	0.418	0.196–0.580
	Pike	20	0.867	0.725–1.01	20	0.894	0.600–1.3	20	0.665	0.290–1.2	19	0.697	0.319–1.4
	Whitefish	20	0.836	0.462–1.25	19	0.858	0.556–1.25	26	1.52	1–2.4	19	1.64	1–3.3
Vicinity of the village of South Indian Lake	Walleye	23	0.872	0.735–1.0	22	0.869	0.400–1.3	25	0.396	0.282–1.00	20	0.406	0.143–0.833
	Pike	21	0.824	0.644–0.981	20	0.825	0.491–1.2	20	0.555	0.275–0.851	20	0.541	0.340–0.724
	Whitefish	21	0.923	0.375–1.5	21	0.828	0.143–1.0	27	1.58	0.875–2.5	20	1.50	0.333–2.1
Region NE of village of South Indian Lake and SW of Missi Falls dam	Walleye	14	0.806	0.685–0.932	14	0.897	0.611–1.1	14	0.449	0.197–0.909	14	0.500	0.206–1.0
	Pike	24	0.832	0.683–0.985	23	0.758	0.295–1.0	24	0.598	0.373–1.1	24	0.544	0.183–0.987
	Whitefish	25	0.795	0.333–1.4	23	0.749	0.455–1.1	24	1.54	0.60–2.9	23	1.45	0.583–2.57
Vicinity of Missi Falls dam	Walleye	4	0.877	0.778–0.964	4	0.996	0.909–1.1	4	0.259	0.244–0.278	4	0.296	0.266–0.354
	Pike	20	0.898	0.745–1.0	19	0.900	0.744–1.0	20	0.561	0.404–0.780	19	0.556	0.370–0.790
	Whitefish	19	0.781	0.25–1.25	19	0.858	0.524–1.6	19	1.60	0.611–2.4	19	1.88	0.923–6.0

of the correlation for whitefish is due to surprisingly low Hg concentrations in specimens from Notigi Lake, where the rise in water level was highest. Evidently, whitefish are much less sensitive than the other fish species to variations in the production of CH_3Hg^+ in their environment. Yet even whitefish displayed a tendency, albeit a weak one, to conform to the same general pattern of variation as the other species, and the Hg in whitefish muscle was predominantly in the form of CH_3Hg^+, as in walleye and pike (Table 3).

Despite their broadly similar responses to regional variations in the extent of postimpoundment flooding, walleye, pike, and whitefish collected from the same sampling sites in the same year (1980) showed different relationships with regionally varying environmental factors. As might be expected, Hg levels in walleye gave significant positive correlations with the CH_3Hg^+ concentrations of fine-grained offshore sediments and overlying surface water (Fig. 3A and 3B). This presumably reflects the fact that most of the Hg absorbed by walleye from their surroundings, whether directly from solution or from food, is in the form of CH_3Hg^+ (Table 3). However, what is not immediately comprehensible is that, although walleye, pike, and whitefish all accumulated CH_3Hg^+ preferentially with respect to inorganic Hg (Table 3), walleye was the *only* species (among these three) whose Hg content correlated significantly with environmental CH_3Hg^+ levels. Hg in pike also gave positive correlations with environmental CH_3Hg^+, but the relationships were insignificant ($P > 0.1$), and Hg in whitefish gave insignificant *inverse* correlations with environmental CH_3Hg^+ ($P > 0.1$). Nevertheless, Hg in pike gave a strong positive correlation with 0.1 M NaOH-extractable iron (Fe) in sediments (Fig. 3C), whilst Hg in whitefish gave a significant negative correlation with sulfide (abbreviated as S^{2-}) in surface water (Fig. 3D).

The difference between the the results for walleye and pike can be explained by the above-mentioned differences in habitat preference and metabolic rate and, perhaps, by a sampling bias. Since most of the sediment and water samples came from the deeper offshore regions of the lake basins, the CH_3Hg^+ data for these samples may be especially representative of the habitat of walleye. Moreover, walleye, owing to their greater propensity for moving from place to place, probably have CH_3Hg^+ body burdens that more accurately reflect the average CH_3Hg^+ concentrations and production rates of the sediments and water in the lakes which they inhabit (Derksen and Green 1987; Jackson 1987). The correlation between Hg in pike and NaOH-extractable Fe in sediment suggests a stronger influence of nearshore regions of flooded land, where terrestrial organic substances — including humic substances, which are NaOH extractable and Fe rich — are concentrated. In the reservoirs, the concentration of NaOH-extractable Fe probably depends largely on the abundance of submerged terrestrial organic matter (both humic and nonhumic) and may therefore be, to a first approximation, an indirect measure of CH_3Hg^+ production in the zone of flooded land. As the pike populations, submerged organic matter, and CH_3Hg^+ are all preferentially concentrated in nearshore regions of the lakes affected by impoundment, the correlation between pike Hg and NaOH-soluble sedimentary Fe in these lakes is understandable. Although the accelerated CH_3Hg^+ production in the zone of flooded land is primarily attributable to nonhumic organic compounds utilised as nutrient substrates by methylating microbes, the refractory humic matter and its associated Fe may also have contributed to the rise in the net rates of microbial CH_3Hg^+ production (Jackson 1989b).

The inverse relationship between whitefish Hg and aquatic S^{2-} suggests that the uptake of Hg by whitefish is limited by environmental sulfides which decrease the bioavailability of the

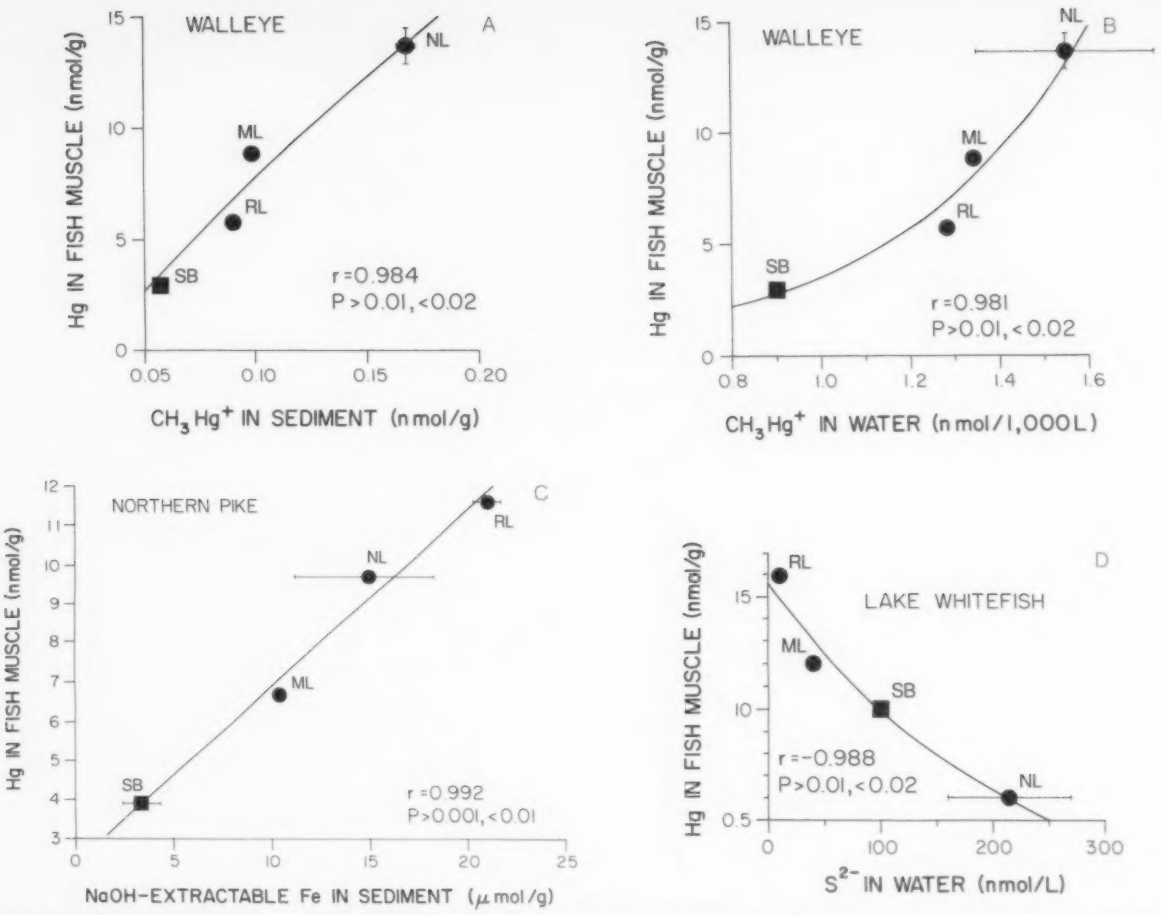

FIG. 3. Relationships between concentrations of (A) Hg in walleye muscle and CH_3Hg^+ in sediment, (B) Hg in walleye muscle and CH_3Hg^+ in centrifuged surface water, (C) Hg in northern pike muscle and NaOH-extractable Fe in sediment, and (D) Hg in lake whitefish muscle and sulfide (S^{2-}) in surface water. The data represent Southern Indian Lake (■) and Notigi Reservoir lakes (●). Dates of sample collection: walleye, pike, and whitefish, 1980; sediments and water for CH_3Hg^+ and S^{2-} analysis, June 1981; sediments for Fe analysis, June and August 1981. See Fig. 2 for abbreviations of field site names.

Hg (Björnberg et al. 1988). The apparent effect of S^{2-} on the accumulation of Hg by whitefish could be an indication that most of the CH_3Hg^+ in whitefish muscle is taken up from ambient water rather than food (see below).

As with walleye, Hg concentrations in shiner correlated significantly with CH_3Hg^+ levels in sediments ($r = 0.850$; $0.05 > P > 0.02$). However, CH_3Hg^+ data were not available for all field sites represented by shiner data, and to make good this deficiency it was necessary to resort to the indirect method of relating the Hg content of the shiner to the nutritional and microbiological factors that control CH_3Hg^+ production. As the rates of CH_3Hg^+ production and bioaccumulation depend primarily on the intensity of heterotrophic microbial activity, which is a function of the abundance of recently submerged organic matter, it might be supposed that Hg levels in shiner would simply rise continuously with increasing organic matter and microbial activity. The results, however, revealed a very different, and more complicated, pattern of variation suggesting interaction of mutually opposing tendencies.

Figure 4 shows Hg concentration in shiner muscle plotted against relative intensity of heterotrophic microbial activity in sediment as estimated by the amount of CO_2 generated per unit dry weight on incubation of fresh sediment samples in the dark under anaerobic conditions (in an atmosphere of N_2) at ~25°C for 10 d (Jackson 1987, 1988b). As the quantity of CO_2 was an indirect measure of the abundance of organic matter capable of supporting microbial growth, it gave strong positive correlations with the quantity of CH_3Hg^+ generated by the microbes in the presence of "available" (reactive) inorganic Hg(II) and with the total organic carbon (C) content of the sediment (Jackson 1987, 1988b). The points in Fig. 4 are segregated into two groups representing (1) Southern Indian Lake and Granville Lake and (2) Notigi Reservoir lakes and East Mynarski Lake. This distinction is not arbitrary; it reflects a clear-cut regional difference in environmental conditions (Table 4; also see Hecky et al. 1987a): the Notigi Reservoir – East Mynarski Lake sites were characterised by well-developed thermal stratification during the summer, low dissolved O_2 levels near the bottom, and sediments with low E_h values, high concentrations of

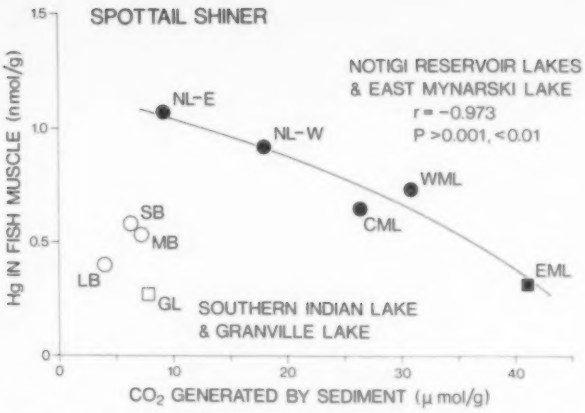

FIG. 4. Relationship between Hg content of spottail shiner muscle and quantity of CO_2 produced by sediment on incubation for 10 d under N_2. The data represent Notigi Reservoir lakes (●), East Mynarski Lake (■), Southern Indian Lake (○), and Granville Lake (□). Dates of sample collection: shiner, 1981 and 1982; sediments, August 1983. See Fig. 2 for abbreviations of field site names.

organic matter, and high rates of CO_2 and CH_3Hg^+ production; in contrast, the Southern Indian Lake – Granville Lake sites displayed litle or no thermal stratification, high dissolved O_2 levels near the bottom, and sediments characterised by higher E_h values, lower concentrations of organic matter, and lower rates of CO_2 and CH_3Hg^+ production. These differences can be attributed both to spatial variations in the extent of flooding and to regional variations in existence before the Churchill River diversion (Bodaly et al. 1984; Hecky et al. 1987a; Jackson 1987, 1988b). The sediments from the three Mynarski lakes yielded the most CO_2 (Fig. 4) and had the highest concentrations of organic C (Jackson 1988b). The Mynarski lake chain, although connected to the Rat River system, through which the redirected Churchill River water is conveyed (Jackson 1988b, fig. 1), lies to one side of the watercourse and is not rapidly flushed; therefore, the lakes are strongly influenced by drainage from the surrounding forest- and muskeg-mantled land. Owing to favourable local conditions, primary production is greater in the East and West Mynarski lakes than in any of the other lakes investigated (Bodaly et al. 1987b; Jackson 1988b).

Results comparable with those shown in Fig. 4 were obtained by plotting the Hg content of shiner against the organic C, total nitrogen (N), S^{2-}, and selenium (Se) concentrations of the sediments and the primary productivity of the water, all of which variables are, like CO_2, linked to organic activity (see data reported by Jackson 1988b). Similar relationships were observed when perch Hg was substituted for shiner Hg. Possibly, walleye and pike fit the same general pattern of variation, but data for additional sampling sites would be needed to verify this. The shiner data are more informative than the data for the other fish species because they represent a larger number of field sites.

As expected, Fig. 4 demonstrates that the CO_2-generating capability of the sediments and the Hg content of shiner were higher in the Notigi Reservoir lakes, where the postimpoundment rise in lake level and organic content was relatively high, than in Southern Indian Lake, where the increase was much smaller, or in Granville Lake, where there was no increase. Surprisingly, however, the most striking feature of the plot is a significant *inverse* correlation for samples from the Notigi Reservoir – East Mynarski Lake sites. The overall shape of the plot could be interpreted as an inverted "V" formed by alternation of two opposing trends: a sharp rise in Hg content with increasing CO_2 up to ~9 μmol CO_2/g (on going from the Southern Indian Lake – Granville Lake sites to Notigi Lake) followed by a gradual decline in Hg content with further increase in CO_2 (from Notigi Lake to East Mynarski Lake). This implies that Hg concentrations in fish rise with increasing abundance of organic nutrient substrates in the sediments until a critical nutrient level is reached and then decline with further enrichment. Thus, the generalisation that Hg levels in reservoir fish have risen in response to recently submerged terrestrial organic matter may be an oversimplification, even though there is a body of convincing evidence in support of it (see literature cited in the introduction).

Laboratory experiments on the effects of an organic nutrient substrate (pulverised sphagnum moss) (Jackson 1987, 1988b) on CH_3Hg^+ production in sediments yielded results comparable with those shown in Fig. 4, implying that the surprising pattern of variation shown by the fish can be explained by nutrient-controlled variations in the nature and activities of the microbial communities in the sediments. On incubation of replicate samples of East Mynarski Lake mud with different quan-

TABLE 4. Physical and chemical characteristics of aquatic environments where spottail shiner were sampled. Values given are ranges. The sediments were collected in 1983. Source of data: Jackson (1988b).

Environmental variable	Sampling region: Southern Indian Lake and Granville Lake	Sampling region: Notigi Reservoir and East Mynarski Lake
Organic C content of sediment (mmol/g)	1.33–2.66	3.08–8.87
E_h of sediment (mV)	−20 to + 50	−94 to −125
O_2 content of bottom water (mg/L)	8.15–9.75	0.75–4.45
CO_2 produced by sediment on incubation under N_2 for 10 d (mg/g)	0.178–0.349	0.405–1.81
CH_3Hg^+ produced by sediment on incubation under N_2 for 10 d (ng/g)	4.96–9.25	12.8–91.1
Degree of thermal stratification in summer	Unstratified or weakly stratified	Moderately to strongly stratified
Temperature at bottom in summer (°C)	16.5–21.0	8.0–14.0

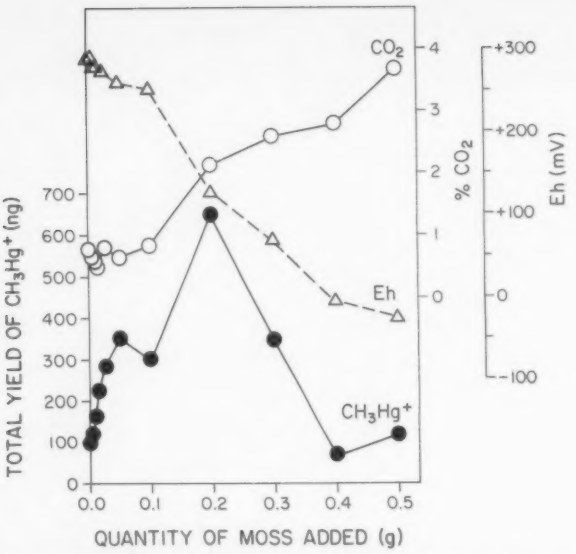

FIG. 5. Effects of varying quantities of nutrient substrate (sphagnum moss) on CH_3Hg^+ (●) and CO_2 (○) production and E_h (Δ) in East Mynarski Lake sediment samples incubated under N_2 for 1 wk in the presence of $HgCl_2$. Date of sample collection: August 1983.

tities of moss for 1 wk under N_2 in the presence of available inorganic Hg(II) (dissolved $HgCl_2$), the quantity of CH_3Hg^+ generated increased with increasing concentration of moss until a maximum was reached and then *declined* sharply to very low values (Fig. 5). Thus, CH_3Hg^+ production was stimulated by small amounts of nutrient supplement but was depressed by large ones. Yet the CO_2 level rose progressively, and the E_h decreased correspondingly, with increasing abundance of nutrient substrate throughout the range of concentrations employed (Fig. 5), demonstrating a continuous increase in overall microbial growth and activity. Therefore, the drop in CH_3Hg^+ content at higher nutrient levels cannot be attributed to a general decline in the vitality of the microbial community. Instead, there must have been a change in the specific activities of the microbes, possibly reflecting ecological succession in the microbial community (Jackson 1989a, 1989b).

Similarly, experiments comparing the effects of nutrient enrichment in sediment samples from different field sites (Fig. 6) showed that supplementary organic nutrients greatly boosted CH_3Hg^+ production in sediments from most of the sites but *lowered* the rate of CH_3Hg^+ production in sediments from East Mynarski Lake and the "flooded forest" zone of Methyl Bay (Southern Indian Lake), the two regions whose sediments had the highest concentrations of organic C and yielded the largest amount of CO_2 on incubation (Jackson 1988b). Apparently it made no difference that most of the organic matter in Methyl Bay sediment consisted of the remains of recently submerged land plants whereas the organic matter in the highly productive East Mynarski Lake sediment was derived largely from the remains of aquatic organisms.

The experimental results (Fig. 5 and 6) suggest that the effect of nutrient enrichment is actually the *net* effect of simultaneous promotion and suppression of CH_3Hg^+ production and that the total abundance of organic matter available for utilisation by microbes determines which of these two opposing processes predominates. Promotion of CH_3Hg^+ production can be attributed to stimulation of the growth and activities of Hg methylating microbes whereas suppression of CH_3Hg^+ production could be ascribed to stimulation of demethylating microbes or reduced availability of inorganic Hg owing to microbial production of Hg-binding agents such as sulfides (as suggested by the drop in E_h) during decomposition of the organic matter.

There is one complicating circumstance which must be borne in mind when comparisons are made between the different field sites as in Fig. 4 and 6: the lakes, and different localities within the same lake, differed from one another even before the Churchill River diversion, and this preexisting environmental variability tends to obscure the regional differences in the impact of impoundment (Jackson 1988a, 1988b). In particular, note that Notigi Reservoir lakes — especially poorly flushed regions, which are strongly influenced by local drainage — were relatively rich in allochthonous organic matter. Although the largest postimpoundment rise in water level (15.2 m) occurred in Notigi Lake, the yields of CO_2 were higher in sediments from the three Mynarski lakes, where there were smaller increases, if any, in water level (0, 6.9, and 9.0 m) (Jackson 1988b), and this is responsible for the negative correlation shown in Fig. 4. Therefore, the significant positive correlation between Hg concentration in fish and rise in lake level (Fig. 2) may be, in part, fortuitous. Because of local conditions predating impoundment, the Mynarski lakes may have had sufficient organic matter to cause partial suppression of CH_3Hg^+ production, with the result that the stimulation of CH_3Hg^+ production in these lakes by organic enrichment due to flooding was less pronounced than if the initial (preimpoundment) concentration of organic matter had been lower. Thus, although the gross difference between Hg levels in Southern Indian Lake and Notigi Reservoir lakes can be attributed to the greater impact of flooding in Notigi Reservoir, the situation observed in the field is probably the net result of complex interactions between effects of flooding and the influence of preflooding environmental conditions.

There could be at least three reasons for the decrease in the Hg content of shiner with an increase in the supply of organic nutrients (and these are not mutually exclusive): (1) "biodilution" or "growth dilution" of Hg (reduction in Hg concentrations in organisms owing to enlargement of the biomass or accelerated growth of individual organisms, respectively) in the more nutrient-rich, productive habitats such as East and West Mynarski lakes (Jernelöv et al. 1975; Huckabee et al. 1979); (2) reduced availability of Hg, and hence a decline in the rates of Hg methylation and bioaccumulation, owing to high concentrations of Hg-binding substances such as sulfides and selenides generated by decomposition of organic matter (Feick et al. 1972; Jernelöv 1972; Turner and Rudd 1983; Jackson 1987, 1988b; Björnberg et al. 1988); and (3) an increase in the activity of Hg demethylating microbes at the expense of Hg methylating microbes.

The biodilution/growth dilution theory cannot be fully evaluated without more biological information, but the available data are at least suggestive. As mentioned above, growth dilution seems to have had detectable, although perhaps minor, effects on both shiner and perch. Hg in shiner from Notigi Reservoir lakes and East Mynarski Lake correlated inversely with primary productivity, as predicted by the biodilution/growth dilution theory, but the relationship is insignificant ($r = -0.719$; $P > 0.1$). Furthermore, there is no evidence for appreciable growth dilution or biodilution in walleye, pike, or whitefish (see above) or in the planktonic and benthic com-

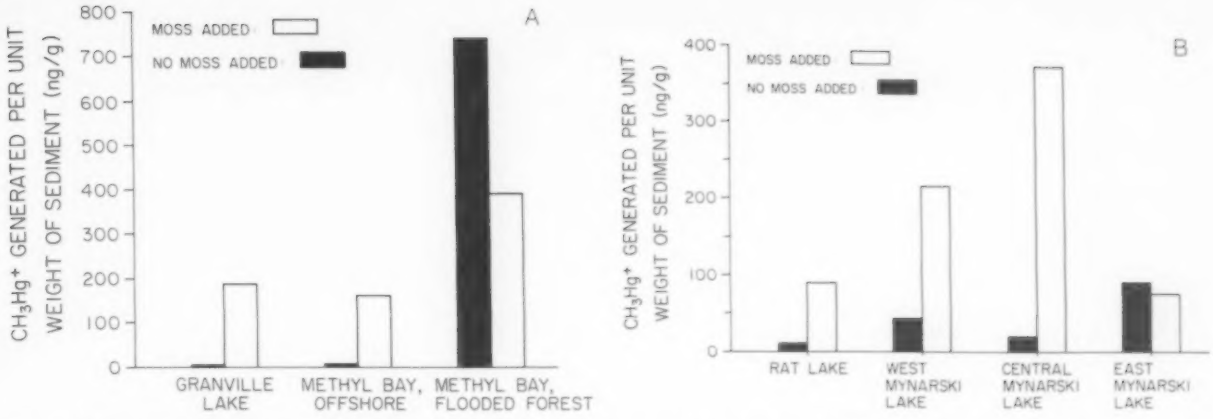

FIG. 6. Quantities of CH_3Hg^+ generated by sediment samples from (A) Granville Lake and Methyl Bay (Southern Indian Lake) and (B) Notigi Reservoir lakes and East Mynarski Lake incubated under N_2 for 10 d in the presence of $HgCl_2$ with and without a nutrient substrate (sphagnum moss). Date of sample collection: August 1983.

munities (Jackson 1988a). In brief, the data suggest that growth dilution is a contributing factor but is of little importance (compare Rudd and Turner 1983).

A significant role for Hg-binding agents is more consistent with the data, although the evidence for it is indirect. The Hg content of shiner in Notigi Reservoir lakes and East Mynarski Lake gave a significant inverse correlation with the Se content of the sediments ($r = -0.881$; $0.05 > P > 0.02$), and, considering the strong affinity of Se^{2-} for Hg and the known effectiveness of Se in interfering with the accumulation of Hg by freshwater fish (Turner and Rudd 1983; Björnberg et al. 1988), this could be construed as indicating that Se depresses Hg bioavailability. There is also support — especially from East Mynarski Lake data — for the belief that sulfides interfered with biological uptake of Hg in the more nutrient-rich environments. East Mynarski Lake sediment had the highest total Hg content and one of the highest rates of CH_3Hg^+ production when incubated with available inorganic (Hg(II) (Jackson 1988b), but East Mynarski Lake shiner had the lowest mean Hg concentration. This paradox can be ascribed to the fact that East Mynarski Lake sediment is anomalously rich in sulfide owing to the lake's high biological productivity (Jackson 1988b).

Finally, a laboratory experiment provided evidence that organic nutrient enrichment may stimulate demethylation as well as methylation in sediments (Fig. 7). Replicate samples of Notigi Lake sediment suspended in aliquots of inorganic Hg(II) solution were incubated under anaerobic conditions for different lengths of time with and without pulverised sphagnum moss. In the absence of moss, CH_3Hg^+ increased abruptly with time but soon levelled off at a low value and remained nearly constant, indicating a brief burst of CH_3Hg^+ production followed by cessation of methylating activity or rapid attainment of a steady state between methylation and demethylation. Yet the CO_2 content of the head gas increased progressively throughout the experiment, implying continuous heterotrophic microbial activity. No CH_4 was detected in any of the head gas samples. In the presence of moss, the maximum yield of CH_3Hg^+ was an order of magnitude higher, but the relative importance of subsequent demethylation was much greater. After a short lag at the outset, the CH_3Hg^+ level rose steeply,

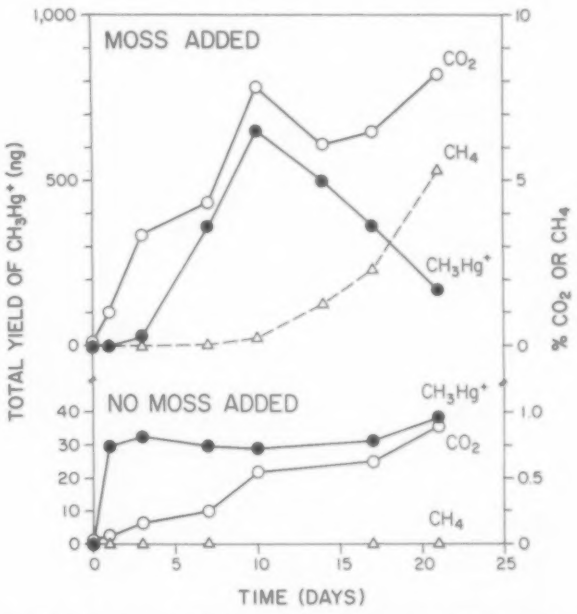

FIG. 7. Production of CH_3Hg^+ (●), CO_2 (○), and CH_4 (Δ) by samples of Notigi Lake (east basin) sediment on incubation under N_2 for varying lengths of time in the presence of $HgCl_2$ with and without a nutrient substrate (sphagnum moss). Date of sample collection: August 1983.

reached a peak, and then declined drastically and continuously. This pattern of variation represents a shift from net production to net decomposition of CH_3Hg^+. The drop in CH_3Hg^+ level coincided with a rise in CH_4 level (compare Jackson 1989b). The CO_2 level rose with increasing CH_3Hg^+ concentration, dipped temporarily when the CH_3Hg^+ content began to fall, and then resumed its rise. These synchronised chemical changes suggest a shift in the species composition of the microbial community ("ecological succession"), with demethylators displacing methylators as the dominant Hg-transforming microbes. The upsurge in CH_4 production accompanying decomposition

of CH_3Hg^+ signals the activation of CH_4 bacteria — presumably reflecting a shift towards more highly anaerobic conditions — and is consistent with the inference that the bacteria were able to transform the methyl group of CH_3Hg^+ into CH_4 (compare Jackson 1989b).

In summary, the relationships illustrated in Fig. 4–7 lead to the conclusion that the effects of the organic nutrient enrichment caused by flooding may be more complex than previously believed. With increasing abundance of nutrient substrates in the sediments, there is a corresponding rise in the rate of CH_3Hg^+ production and bioaccumulation until a maximum is reached at a critical nutrient level, beyond which the rate comes back down owing to the rising importance of Hg demethylating microbes and Hg-binding agents such as sulfides and selenides generated during decomposition of the organic matter. Even in lakes initially rich in organic nutrients, the additional enrichment caused by flooding stimulated the production and bioaccumulation of CH_3Hg^+, but this effect was probably less pronounced than it would have been if the initial supply of organic matter had been smaller.

"Relative rates of CH_3Hg^+ production" in sediments, and their ability to predict Hg levels in fish

The relationships between Hg levels in fish and relative rates of CH_3Hg^+ production in fine-grained offshore sediments at different sampling sites were examined. Besides providing further information on the transfer of Hg from sediments to different kinds of fish under varying environmental conditions, this study tested the validity, ecological relevance, and potential practical utility of the methods used for quantifying in situ CH_3Hg^+ production, and also tested the suitability of the fish species for whole-lake Hg bioassays.

The CH_3Hg^+ assay technique employed in the experiments discussed previously was adapted for measurement and comparison of the potential Hg methylating capabilities of sediments from different field sites (Jackson 1987, 1988b, 1989b; compare Furutani and Rudd 1980; Furutani et al. 1984; Hecky et al. 1987a; Ramsey and Ramlal 1987a, 1987b). However, this method alone is not sufficient to estimate the relative rates at which CH_3Hg^+ is actually generated in field environments, as it only measures the ability of the sedimentary microflora to generate CH_3Hg^+ from an arbitrary fixed quantity of artificially added available inorganic Hg(II) under standardised conditions ("available," in this context, meaning capable of reacting to form CH_3Hg^+). It does not take the abundance of available inorganic Hg(II) in the sediment under natural conditions into account. Therefore, an empirical method for estimating the relative rate of CH_3Hg^+ production in sediment was developed (Jackson 1987, 1988b), and the ability of this parameter to predict Hg levels in fish was tested. The technique involved performance of separate laboratory assays for (1) the "Hg methylating capability" of the sediment (CH_3Hg^+ generated per unit dry weight of sediment on incubation of 10 g of fresh sediment with 20 mL of 10 μM $HgCl_2$ solution under N_2 in the dark at ~25°C for 10 d) and (2) the "available inorganic Hg" content of the sediment (represented either by the Hg fraction extracted with N_2-purged 0.5 M $CaCl_2$ *or* by the total Hg/Se or total Hg/S^{2-} ratio of the sediment). The values for the two parameters were then multiplied to give a compound variable defined as the "relative rate of CH_3Hg^+ production." The procedures employed for quantifying the available inorganic Hg were based on two premises: (1) that the available inorganic Hg pool is weakly adsorbed to sediment particles and is therefore extractable with mild solvents and (2) that the availability of sediment-bound inorganic Hg is limited mainly by sulfides and selenides owing to their tendency to form exceptionally strong covalent bonds with Hg. Both assumptions are consistent with current knowledge of the factors that control Hg availability (D'Itri 1972; Gavis and Ferguson 1972; Jernelöv 1972; Wood 1974; Bisogni and Lawrence 1975; Rimerman et al. 1977; Beijer and Jernelöv 1979; Turner and Rudd 1983; Jackson 1987, 1988b; Björnberg et al. 1988).

The Hg content of walleye muscle gave significant positive correlations with all three estimates of the relative rate of CH_3Hg^+ production (Fig. 8), and, as expected, the intensity of CH_3Hg^+ generating activity increased in the order Granville Lake < Southern Indian Lake < Notigi Reservoir lakes. The three compound variables gave much more significant correlations than did the simple variables of which they were composed (Table 5), demonstrating that the net rate of Hg accumulation by the fish depends on the *combined* effect of the abundance of available inorganic Hg and the rate at which the microflora is able to transform this Hg into CH_3Hg^+, and not on either of these variables alone (compare Jackson 1987, 1988b). The $CaCl_2$-extractable Hg and Hg/S^{2-} data used in Fig. 8A and 8B are the mean values for samples collected in June and August 1981, but the contributions of these variables to the significance of the correlations are due mainly to the August values. Consequently, the significance of the correlations is considerably higher if the August data alone are used (Fig. 9), even though there are fewer data for August.

Walleye was the only fish species whose Hg content correlated significantly with the relative rate of CH_3Hg^+ production (Table 6). According to these results and other data presented above (Fig. 3A and 3B), walleye is the most suitable species for utilisation in bioassays for quantitative comparative study of the speciation, bioavailability, and biogeochemical pathways of Hg in whole lakes, or at least in the zone of fine-grained offshore sediments which cover the widest areas of lake bottom. Probably the reason for the unique suitability of this species is that walleye move rapidly and freely through extensive regions of open water, with the result that their CH_3Hg^+ body burdens are strongly dependent on the average CH_3Hg^+ production rates and concentrations of the lakes which they inhabit (Derksen and Green 1987; Jackson 1987). Thus, it would seem that walleye are exceptionally good lakewide "integrators" of the factors that control environmental CH_3Hg^+ production. At the opposite extreme are the whitefish, which gave the least significant relationship (Table 6).

As demonstrated by its correlation with Hg in walleye, the relative rate of CH_3Hg^+ production is an ecologically meaningful parameter which can be utilised for comparative study of Hg speciation and bioavailability in different aquatic environments. Thus, it is potentially useful for assessment of habitat alterations and environmental management decisions from the standpoint of their adverse or beneficial effects on the biogeochemical pathways of Hg. It also implies that $CaCl_2$-extractable Hg and the Hg/S^{2-} and Hg/Se ratios are reliable parameters for estimating the concentration of available inorganic Hg or relative availability of inorganic Hg in sediment. More work, however, is needed to characterise the $CaCl_2$-extractable inorganic Hg species and delineate their biogeochemical cycles. Little is known about the forms of inorganic Hg in nature; and, although a number of mild selective solvent extraction techniques have been used to extract "available inorganic Hg" from sediments (Jackson 1984, 1987, 1988a, 1988b; Jackson and

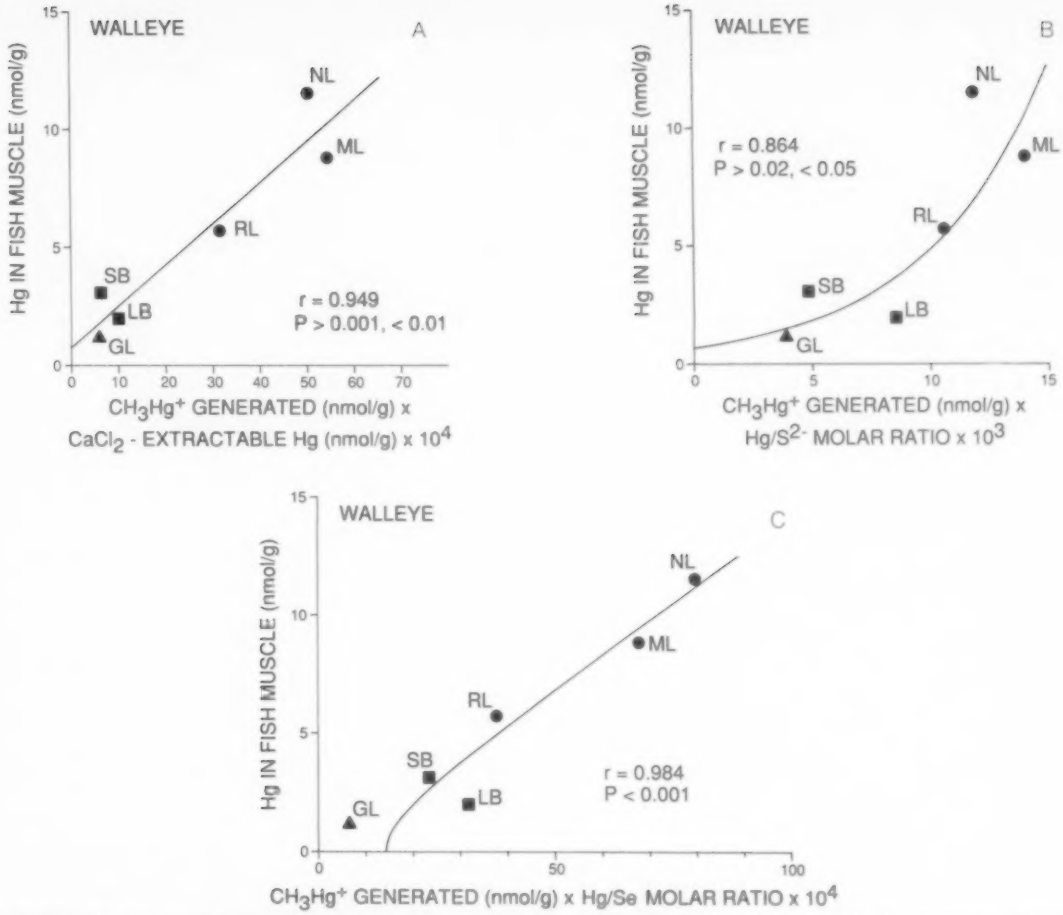

FIG. 8. Relationship between Hg content of walleye muscle and relative rate of sedimentary CH_3Hg^+ production as represented by the "Hg methylating capability" of sediment multiplied by the sediment's (A) $CaCl_2$-extractable Hg concentration, (B) Hg/S^{2-} ratio, or (C) Hg/Se ratio. The data represent Granville Lake (▲); Southern Indian Lake (■); and Notigi Reservoir lakes (●). Dates of sample collection: fish, 1980 and 1981; sediment analysed for methylating capability and Hg/Se ratio, August 1983; sediment analysed for $CaCl_2$-extractable Hg and Hg/S^{2-} ratio, June and August 1981. See Fig. 2 for abbreviations of field site names.

Woychuk 1980a, 1980b; Jackson et al. 1980, 1982), there is not much information on the biological significance of the Hg species isolated. Therefore, the comparison between sediment assay data and fish data was particularly instructive from the standpoint of assessing the bioavailability of the extracted Hg. Note that the procedure for selective solvent extraction must be chosen with care. Unlike $CaCl_2$, neither DTPA nor dilute acetic acid was found to be satisfactory, suggesting that $CaCl_2$ released available Hg from the sediments by the formation of soluble Hg chloride complexes (Jackson 1988b). It should also be pointed out that $CaCl_2$-extractable Hg was consistently more abundant in August than in June (Jackson 1988b). This seasonal effect suggests accelerated conversion of unavailable Hg into available species during the summer, possibly owing to enhanced microbial activity leading to accelerated decomposition of organic matter and reduction and dissolution of ferric oxyhydroxide, accompanied by release of Hg bound to these substances.

It may be mentioned, too, that the sediments gave a highly significant positive linear correlation between total Hg and S^{2-} (for June 1981 samples, $r = 0.967$; $P < 0.001$) with very little scatter, and the regression line, for all practical purposes, intersected the origin of the graph (Jackson 1988b). Similarly, Hg was highly covariant with Se ($r = 0.985$; $P < 0.001$) in all samples but those from the geochemically anomalous Granville Lake and west basin of Notigi Lake, where the Hg/Se ratios were aberrantly low (0.063 and 0.043, respectively, as opposed to a range of 0.15–0.27 for all other sampling sites). (Granville Lake and the west basin of Notigi Lake were the only sites where manganese nodules were found; this implies exceptionally vigorous mixing and aeration by fluvial currents, suggesting mobilisation and loss of Hg through oxidation of sulfides and selenides but without a corresponding loss of total Se. By the same token, the proportion of the total Hg that was extractable with $CaCl_2$ was highest in regions of strong current action and aeration (Jackson 1988b).) Furthermore, all sediments contained more than enough sulfide and Se to bind 100% of the Hg (Jackson 1988b). These observations, together with the well-known preferential affinity of Hg for sulfides and selenides, support the inference that most of the sedimentary Hg

TABLE 5. Correlation matrix indicating relationship between Hg content of walleye muscle (mean for 1980 and 1981) and various geochemical parameters representing sediment samples collected in 1981 and 1983. r = correlation coefficient; P = significance probability; $\bar{X}$ = mean.

Parameter tested	r	P
[Hg methylating capability (Aug. 1983)] × [$CaCl_2$-extractable Hg ($\bar{X}$, June and Aug. 1981)]	0.949	>0.001, <0.01
[Hg methylating capability (Aug. 1983)] × [Hg/S^{2-} ratio ($\bar{X}$, June and Aug. 1981)]	0.864	>0.02, <0.05
[Hg methylating capability (Aug. 1983)] × [Hg/Se ratio (Aug. 1983)]	0.984	<0.001
Hg methylating capability (Aug. 1983)	0.837	>0.05, <0.1
$CaCl_2$-extractable Hg ($\bar{X}$, June and Aug. 1981)	0.905	>0.01, <0.02
[Hg methylating capability (Aug. 1983)] × [Total Hg ($\bar{X}$, June and Aug. 1981)]	0.796	>0.05, <0.1
Total Hg ($\bar{X}$, June and Aug. 1981)	0.720	>0.1
S^{2-} ($\bar{X}$, June and Aug. 1981)	0.668	>0.1
Total Hg (Aug. 1983)	0.874	>0.02, <0.05
Se (Aug. 1983)	0.399	>>0.1
[Hg methylating capability (Aug. 1983)] × [Total Hg (Aug. 1983)]	0.884	>0.01, <0.02 (~0.02)

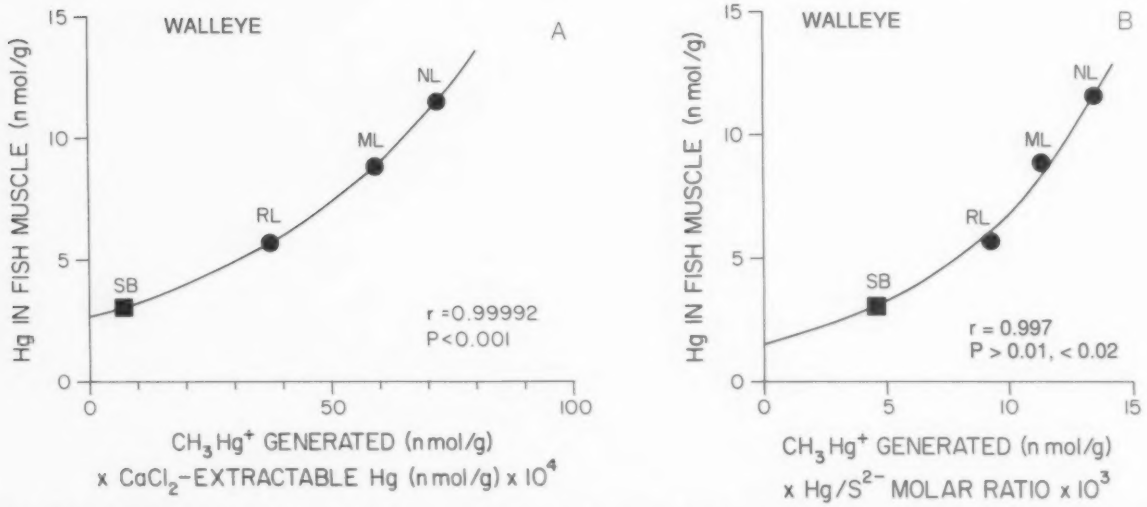

FIG. 9. Relationship between Hg content of walleye muscle and relative rate of sedimentary CH_3Hg^+ production as represented by the "Hg methylating capability" of the sediment multiplied by the sediment's (A) $CaCl_2$-extractable Hg content or (B) Hg/S^{2-} ratio. The data represent Southern Indian Lake (■) and Notigi Reservoir lakes (●). Dates of samples collection are the same as in Fig. 8 except that the $CaCl_2$-extractable Hg and Hg/S^{2-} ratio values represent only the sediment samples collected in August 1981. See Fig. 2 for abbreviations of field site names.

TABLE 6. Correlation matrix relating the mean Hg content of muscle tissue of different species of fish to the rate of CH_3Hg^+ production in bottom sediments (as represented by the parameter [Hg methylating capability] × [$CaCl_2$-extractable Hg concentration]). r = correlation coefficient; P = significance probability.

Fish species	r	P
Walleye	0.949	>0.001, <0.01
Pike	0.825	>0.05, <0.1
Whitefish	0.566	>>0.1
Shiner	0.794	>0.05, <0.1
Perch	0.940[a]	>0.1[a]

[a]Based on data from only three sampling sites.

was bound to sulfides and selenides and was therefore not readily available for methylation. The small pool of available Hg was probably adsorbed to binding sites other than those containing sulfide or reduced Se.

Role of Diet and "Food Chain" Effects

Reference has been made to the anomalously weak effect of environmental CH_3Hg^+ production on the accumulation of Hg by whitefish. Could this peculiarity be a reflection of low CH_3Hg^+ concentrations in the food consumed by these fish? An attempt was made to find an answer by examining the role of benthic invertebrates, the staple of the whitefish diet. The influence of the benthic fauna was assessed indirectly by com-

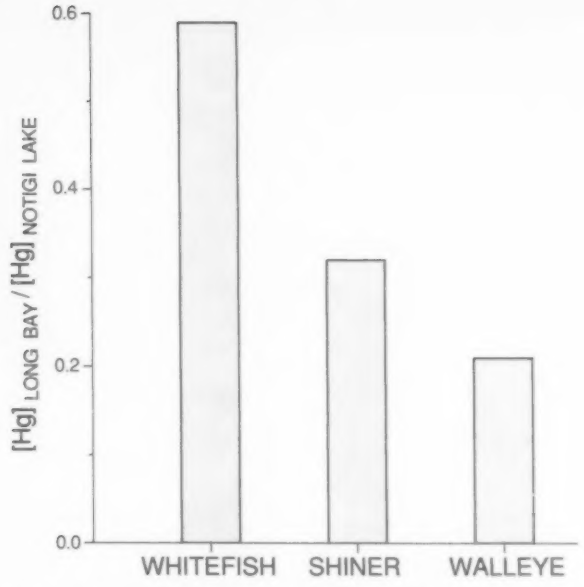

FIG. 10. Values of the ratio of mean Hg content of fish muscle in Long Bay (Southern Indian Lake) to mean Hg content of fish muscle in Notigi Lake computed for lake whitefish, spotttail shiner, and walleye sampled in 1981.

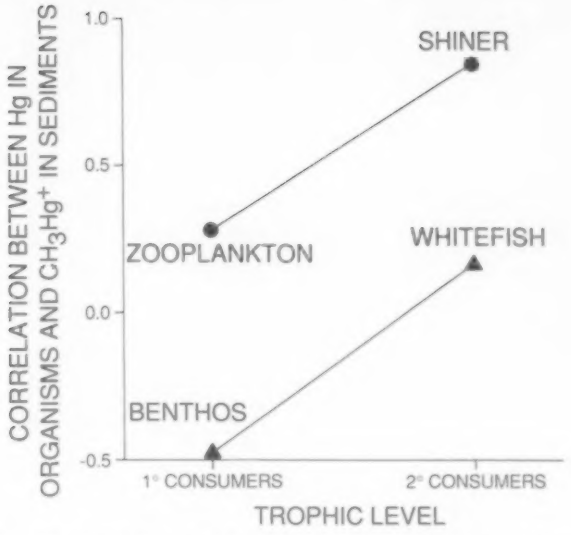

FIG. 11. Correlation coefficients representing degree of association between the Hg content of biological specimens (>73 μm zooplankton, benthic invertebrates, spottail shiner muscle, and lake whitefish muscle) and the CH_3Hg^+ content of sediments in different lakes plotted against the trophic level of the organisms. Dates of sample collection: sediments, plankton, and benthos, June 1981; whitefish, 1980 and 1981; shiner, 1981 and 1982.

puting the ratio of the Hg content of fish from Long Bay (Southern Indian Lake) to the Hg content of Notigi Lake fish and comparing the ratio values for different species of fish (omitting perch and pike, which were not found in Long Bay). The rationale for employment of this ratio lies in the surprising fact that Hg concentrations in benthic chironomid larvae, oligochaetes, nematodes, and pelecypods were highest in Long Bay and much lower in Notigi Lake and other Notigi Reservoir lakes (Jackson 1988a), even though sedimentary CH_3Hg^+ levels and production rates were higher in the latter (Jackson 1988b).

Whitefish had the highest ratio (Fig. 10), suggesting that the Hg content of their food had a significant effect on their rate of Hg assimilation. Shiner gave the second highest ratio, probably reflecting the fact that their diet includes benthic organisms (McCann 1959; Price 1963; Scott and Crossman 1973; Yager and McComish 1976; Anderson and Brazo 1978; Wells 1980); and, understandably, walleye, which feed on other fish (Scott and Crossman 1973), gave the lowest ratio (Fig. 10).

The contribution of diet to the Hg content of fish was also investigated by computing correlation coefficients relating Hg in shiner, whitefish, benthos, and >73 μm zooplankton to CH_3Hg^+ in associated sediments and then plotting each value against the trophic level of the organism (Fig. 11). In this plot, which is intended as a visual aid to illustrate the accumulation of CH_3Hg^+ up food chains, zooplankton and shiner form a food chain segment linking the primary and secondary consumer levels, whilst benthos and whitefish form a separate but equivalent food chain segment; as anticipated, the positions of the points imply greater concentrations of CH_3Hg^+ at higher trophic levels. This model is admittedly an oversimplification, as the diets of the two fish species are variable and overlap somewhat (McCann 1959; Price 1963; Smith and Kramer 1964; Basch 1968; Anderson and Smith 1971; Scott and Crossman 1973; Yager and McComish 1976; Anderson and Brazo 1978; Wells 1980), but on the basis of what is known about the feeding habits of shiner and whitefish at the stages of development represented by the specimens, it is useful for purposes of comparison. The plankton–shiner chain lies above the benthos–whitefish chain and essentially parallel to it, suggesting that the relatively feeble effect of environmental CH_3Hg^+ production on the accumulation of Hg by whitefish is at least partly due to a paucity of CH_3Hg^+ in the benthic invertebrates on which they feed (Jernelöv and Lann 1971; Jackson 1988a). Apparently, zooplankton had a greater abundance of CH_3Hg^+, resulting in correspondingly high concentrations in shiner.

Although the results presented above suggested that the Hg levels in whitefish and shiner depend appreciably on Hg uptake from food, other observations seem to indicate that diet has only a minor effect on Hg concentrations in whitefish. Thus, Hg in whitefish, surprisingly, gave a significant *negative* correlation with Hg in benthic invertebrates (Table 7; Fig. 12A). In contrast, Hg in shiner, as expected from the model shown in Fig. 11, correlated positively with Hg in >73 μm plankton (Fig. 12B). Plankton collected in June (during the spring flood) gave a significant correlation whereas plankton collected in August gave a very insignificant correlation, but in both cases the correlations were *positive* (Table 7). By the same token, CH_3Hg^+ levels in sediments correlated inversely with Hg in benthic invertebrates but positively with Hg in >73 μm plankton (Jackson 1988a). The relationships are weak ($P > 0.1$), but they are useful for purposes of comparison; they imply that benthic invertebrates are far less important than zooplankton as vehicles for transferring CH_3Hg^+ to fish.

These findings suggest that whitefish and shiner differ profoundly in their Hg uptake and elimination pathways. The results are consistent with the following working hypothesis: whitefish accumulate Hg mainly by direct absorption of dis-

TABLE 7. Correlation matrix relating the Hg content of lake whitefish and spottail shiner muscle to the Hg content of benthic invertebrates and >73 μm zooplankton from the same sampling sites. r = correlation coefficient; P = significance probability; $\bar{X}$ = mean.

	Hg in benthos		Hg in >73 μm plankton			
	June 1981		June 1981		August 1981	
	r	P	r	P	r	P
Hg in whitefish ($\bar{X}$ for 1980 and 1981)	−0.897	> 0.02, < 0.05	—	—	—	—
Hg in shiner ($\bar{X}$ for 1981 and 1982)	—	—	0.726	>0.02, <0.05	0.224	>>0.1

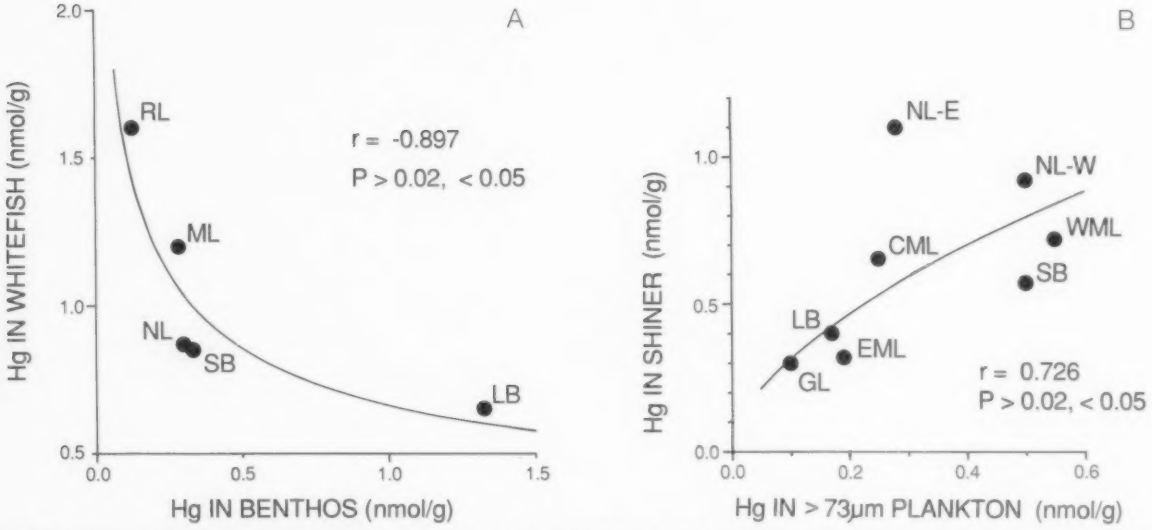

FIG. 12. Relationships between Hg concentrations in (A) lake whitefish muscle and benthic invertebrates and (B) spottail shiner muscle and >73 μm zooplankton in various lakes. Dates of sample collection: whitefish, 1980 and 1981; benthos and plankton, June 1981; shiner, 1981 and 1982. The Hg level in the benthos was computed as the weighted sum of Hg concentrations of individually analysed component species. See Fig. 2 for abbreviations of field site names.

solved CH_3Hg^+ from water through the gill membrane whereas Hg ingested with food is mostly excreted (although the contribution of dietary Hg is not negligible, as implied by Fig. 10 and 11); in contrast, shiner absorb major amounts of Hg from both food and water. Even though the Hg in whitefish is mainly in the form of CH_3Hg^+ (Table 3), most of the Hg in the benthic invertebrates on which the fish feed is probably inorganic and is therefore excreted preferentially (Jernelöv and Lann 1971; Jackson 1988a).

Returning to "food chain" effects, the concentrations of Hg in walleye and pike, as might be expected, were considerably higher than those in shiner, whitefish, and perch (Table 1). This reflects the fact that the fish-eating predators walleye and pike occupy the highest trophic level. CH_3Hg^+ undergoes "biomagnification" up the aquatic food chain, with the result that organisms at the upper end of the chain generally have the highest CH_3Hg^+ and total Hg concentrations (Klein and Goldberg 1970; Jernelöv and Lann 1971; Gavis and Ferguson 1972; D'Itri 1972; Peakall and Lovett 1972; Windom and Kendall 1979), although exceptions have been noted (Knauer and Martin 1972). However, more refined comparison of the data demonstrated that the concept of accumulation up the food chain is an oversimplification. Although pike and walleye are at the same trophic level and have similar diets and feeding habits (Scott and Crossman 1973), they showed different spatial and temporal variations in Hg content (see above). In addition, shiner consistently had higher Hg concentrations than perch even though they belonged to the same trophic level and had similar fork lengths (Table 1). (When fully grown, perch are larger than shiner and prey on them, and thus are above them in the food chain (W. Liaw, pers. comm.), but the shiner and perch specimens dealt with in this paper were apparently not fully grown, and both were presumably feeding on benthic and planktonic invertebrates and other small aquatic organisms such as fish larvae (Tharratt 1959; Price 1963; Smith and Kramer 1964; Keast and Webb 1966; Anderson and Smith 1971; Scott and Crossman 1973; Yager and McComish 1976; Thorpe 1977; Anderson and Brazo 1978; Ney 1978; Wells 1980; Hubert and Sandheinrich 1983; Chabot and Maly 1986).) These observations demonstrate that the tendency of Hg concentration to increase up the food chain is modified by inherent differences between individual species and variations in the physicochemical environment. In general, the distribution of Hg among different aquatic species is not simply a function of relative posi-

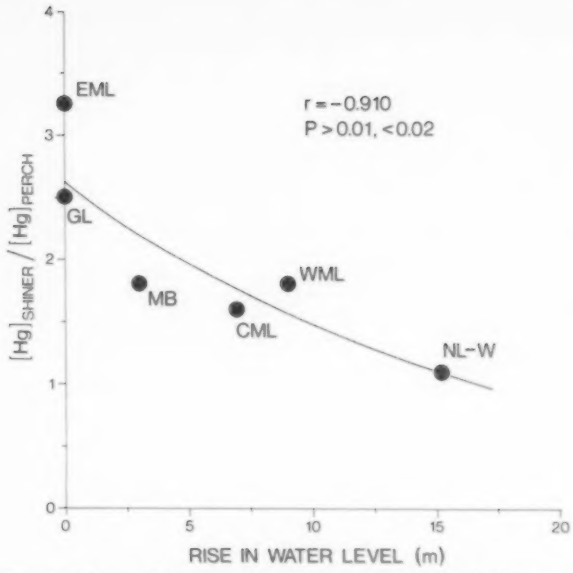

FIG. 13. Values of the ratio of Hg concentration in spottail shiner muscle to Hg concentration in yellow perch muscle at different field sites plotted against the rise in water level following impoundment and diversion of Churchill River water. See Fig. 2 for abbreviations of field site names.

tion in the food chain (or food web), as other biological factors such as diet, behaviour, habitat preference, metabolic rate, age, size, growth rate, and mechanisms of excretion, together with environmental variables such as temperature and pH, also affect Hg bioaccumulation (D'Itri 1972; Knauer and Martin 1972; Scott and Armstrong 1972; de Freitas et al. 1974, 1977; Reinert et al. 1974; Scott 1974; de Freitas and Hart 1975; Ruohtula and Miettinen 1975; Norstrom et al. 1976; Huckabee et al. 1979; Derksen and Green 1987; Hecky et al. 1987a). The biomagnification of CH_3Hg^+ up the food chain may, in fact, be due largely to the longer life spans and lower growth rates of animals at the higher trophic levels rather than trophic effects as such (de Freitas et al. 1974; Huckabee et al. 1979).

Now let us consider possible causes of the systematic differences in Hg content between fish species at the same trophic level — specifically, between shiner and perch and between walleye and pike. A reasonable working hypothesis is that differences in biological factors like food selection and habitat preference caused these species to respond differently to spatially varying ambient conditions or to be exposed to different environmental influences, even within the same lake.

The ratio $[Hg]_{shiner}/[Hg]_{perch}$ (Hg content of shiner divided by Hg content of perch) decreased as the postimpoundment rise in lake level increased (Fig. 13). In lakes unaffected by flooding, Hg concentrations were 2.5–3.25 times higher in shiner than in perch, but where the impact of flooding was greatest (in Notigi Lake), the two species had nearly equal Hg concentrations. Yet the Hg levels in both species increased with rise in lake level (Fig. 2), indicating that the responses of the two species to flooding were essentially the same and differed from one another only in degree. The observed variation in the $[Hg]_{shiner}/[Hg]_{perch}$ ratio with respect to the extent of flooding may reflect different responses of the two species to previously reported effects of flooding on the nature and abundance of the planktonic and benthic organisms consumed by these species (Patalas and Salki 1984; Wiens and Rosenberg 1984). Thus, shiner and perch may have manifested different regional variations in diet, growth rate, metabolic rate, and biomass — and hence differences in Hg uptake, elimination, and biodilution kinetics — with the result that the proportion of shiner Hg to perch Hg changed as a function of the degree of environmental alteration due to flooding. A difference in food selection or rate of food intake might conceivably have caused the observed effect.

In contrast, the ratio $[Hg]_{walleye}/[Hg]_{pike}$ (Hg content of walleye divided by Hg content of pike) increased progressively as the organic C/silt and clay/quartz ratios of the sediment increased (Fig. 14) but was not closely linked to the postimpoundment rise in lake level owing to the low ratio value for Rat Lake. Walleye Hg exceeded pike Hg in Notigi Lake and the Mynarski lakes, all of whose sediments are rich in organic matter; but the reverse was true in Granville Lake, South Bay of Southern Indian Lake, and Rat Lake, all of whose sediments are poor in organic matter and correspondingly rich in mineral detritus (Fig. 14 and 15) (Jackson 1988b). The sediments of South Bay and Rat Lake (the receiving basin for the outflow from South Bay) have especially high proportions of quartz and silt because of rapid erosion of Pleistocene silty clay deposits along the shore of South Bay, and Granville Lake sediment has a high mineral content because the lake is a receiving basin for detritus-laden Churchill River water (Jackson 1988a, 1988b). As all sediment samples consisted of mud mixed with little or no sand (Jackson 1988b), the silt fraction presumably accounted for most of the quartz. Note that the ratio $[Hg]_{walleye}/[Hg]_{pike}$ correlated *positively* with clay and organic C but *inversely* with quartz and silt, although it correlated less strongly with clay, quartz, organic C, and silt individually than with the clay/quartz and organic C/silt ratios (Table 8). Moreover, the relationships of the fish Hg ratio with sediment composition are due almost entirely to variations in walleye Hg (Table 8). The separate $[Hg]_{walleye}$ and $[Hg]_{pike}$ data varied in a complex manner with respect to sediment composition (Fig. 15), declining sharply with increasing organic C/silt ratio until a minimum was reached and then increasing with a further increase in the ratio.

Quartz and silt correlated positively, if rather weakly, with dolomite (Table 9), indicating that they are largely derived from eroded local deposits of the Pleistocene silty clay, which contains dolomite (Jackson 1988b); but clay and organic C were inversely related to dolomite (Table 9). Thus, fine-grained sediments rich in silt-sized quartz represent waters characterised by abundant suspended silt and rapid deposition of mineral detritus owing to shoreline and river bank erosion, whilst sediments richer in clay and organic matter represent waters where the influence of shoreline and bank erosion has been slight or negligible and the suspended particles are therefore composed mainly of organic matter together with relatively small amounts of mineral detritus consisting largely of clay.

The observation that Hg levels were higher in walleye than in pike at sites where the sediments had high organic C and low silt or quartz concentrations can be attributed to interactions of physiological factors controlling the behaviour and spatial distribution of the fish with environmental factors that determine spatial variation in the rate of CH_3Hg^+ production. In the reservoirs, CH_3Hg^+ production is stimulated by organic matter in the nearshore zone of recently submerged land but has been depressed locally by silt and clay eroded from shoreline deposits (Jackson 1988b). Pike mainly inhabit shallow nearshore waters,

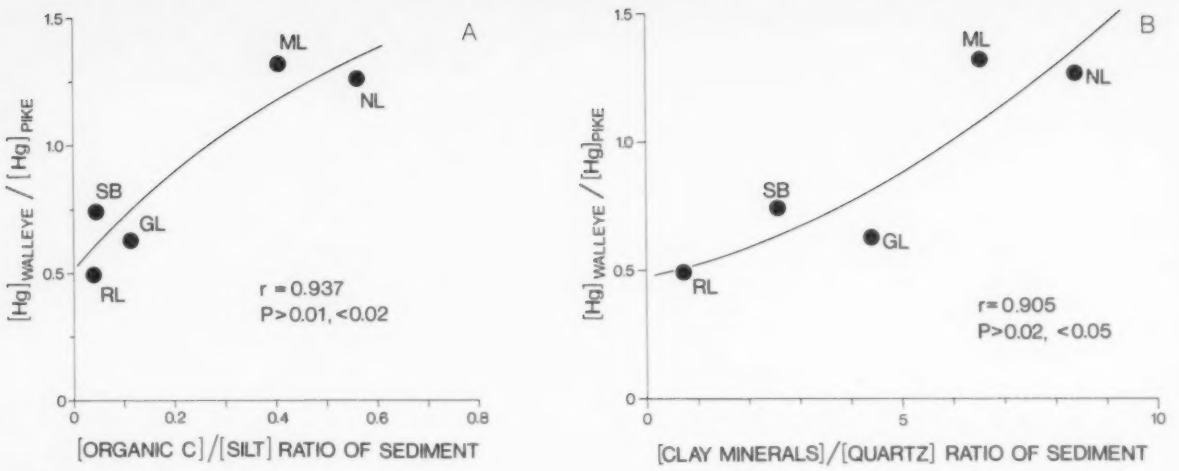

FIG. 14. Relationships between the ratio of Hg concentration in walleye muscle to Hg concentration in northern pike muscle and the (A) organic C/silt and (B) clay/quartz ratios of the sediments in various lakes. See Fig. 2 for abbreviations of field site names.

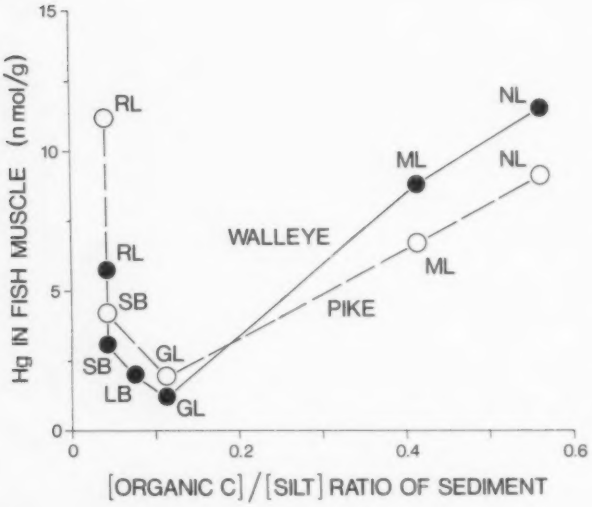

FIG. 15. Relationships between the concentrations of Hg in walleye (●) and northern pike (○) muscle and the organic C/silt ratio of sediment in various lakes. See Fig. 2 for abbreviations of field site names.

where, in recently formed reservoirs, the rates of CH_3Hg^+ production are high whereas walleye presumably spend part of their time in offshore waters, where the rates are lower. In Southern Indian Lake, where the zone of flooded land is narrow (because the postimpoundment rise in water level was small), this behavioural difference may well cause the rate of Hg bioaccumulation to be higher in pike than in walleye. However, in Notigi Lake and the West and Central Mynarski lakes, where the zone of flooded land is wider (because the postimpoundment rise in water level was large), walleye undoubtedly spend more time in regions of high CH_3Hg^+ production rates than is the case in Southern Indian Lake; therefore, in these lakes the difference in spatial distribution of walleye and pike must have less effect on relative rates of Hg uptake by these fish, and so the countervailing effect of some other factor such as the higher metabolic rate of walleye may cause the rate of Hg bioaccumulation to be higher in walleye than in pike (Hg uptake rate being a function of metabolic rate (Reinert et al. 1974; de Freitas and Hart 1975; Norstrom et al. 1976)). In Rat Lake, as in other Notigi Reservoir lakes, the zone of flooded land is relatively wide, but its effect was apparently negated by the large amounts of suspended silt introduced into the lake from South Bay (Fig. 14).

Conceivably the difference between Hg levels in walleye and pike may, to some extent, reflect other spatially varying ecological factors such as (1) the occurrence of high concentrations of allochthonous organic matter in poorly flushed nearshore waters fed by drainage from local forest soils and muskeg and (2) the tendency of some species of zooplankton to avoid the littoral zone whilst others are concentrated there, and the generally poor development of typical pelagic zooplankton communities near the shore (Ruttner 1963; Hutchinson 1967).

Biochemical Mechanisms for Excretion of CH_3Hg^+

The partitioning of CH_3Hg^+ between the liver and muscle tissue of whitefish, walleye, and pike in four widely separated regions of Southern Indian Lake was investigated in order to compare the metabolic pathways of Hg in these species. (Shiner and perch could not be included in the study owing to a lack of information on Hg in their livers.) The data (Table 3) provide indirect support for the hypothesis that a major reason for the anomalously weak tendency of whitefish to accumulate CH_3Hg^+ from their surroundings is that this species possesses an efficient special biochemical mechanism for excretion of CH_3Hg^+ (see p. 2453).

The mean $[CH_3Hg^+]_{liver}/[CH_3Hg^+]_{muscle}$ ratios (CH_3Hg^+ content of liver divided by CH_3Hg^+ content of muscle) at the four sampling sites were consistently much higher in whitefish (1.45–1.88) than in walleye and pike (0.296–0.697), and total Hg data for liver and muscle gave essentially the same result (Table 3). Walleye yielded the lowest ratio values, but the values for walleye and pike did not differ widely. The ratio values for the three species gave significant inverse correlations with the correlation coefficients representing the relationships

TABLE 8. Correlation matrix relating Hg concentrations in walleye and pike, and the ratio of walleye Hg to pike Hg, to the composition of associated sediments in northern Manitoba lakes. The fish data are mean values for 1980 and 1981, and the sediments were sampled in 1983. Long Bay (Southern Indian Lake) is not represented because no pike were sampled there. r = correlation coefficient; P = significance probability.

	Clay/quartz ratio of mineral fraction of sediment		Clay mineral content of mineral fraction of sediment		Quartz content of mineral fraction of sediment		Organic C/silt ratio of sediment		Organic C content of sediment		Silt content of sediment	
	r	P	r	P	r	P	r	P	r	P	r	P
Walleye Hg/ Pike Hg	0.905	>0.02, <0.05	0.852	>0.05, <0.1	−0.890	>0.02, <0.05	0.937	>0.01, <0.02	0.812	>0.05, <0.1	−0.801	>0.1
Walleye Hg	0.904	>0.02, <0.05	0.731	>0.1	−0.469	>>0.1	0.972	>0.001, <0.01	0.609	>>0.1	−0.674	>>0.1
Pike Hg	−0.399	>>0.1	−0.466	>>0.1	0.700	>0.1	0.364	>>0.1	0.206	>>0.1	−0.534	>>0.1

TABLE 9. Correlation matrix relating the silt, quartz, clay, and organic C content of northern Manitoba lake sediments to the dolomite content of the sediments. The sediment samples were collected in 1983 (Jackson 1988b). r = correlation coefficient; P = significance probability.

	Dolomite in mineral fraction of sediment	
	r	P
Silt content of sediment	0.521	~0.1
Quartz content of mineral fraction of sediment	0.537	>0.05, <0.1
Clay content of mineral fraction of sediment	−0.546	>0.05, <0.1
Organic C content of sediment	−0.690	>0.01, <0.02

between the Hg content of fish muscle and the concentrations of CH_3Hg^+ in the sediment and water, the Hg methylating capability of the sediment, and the relative rate of CH_3Hg^+ production in the sediment (Fig. 16). Ostensibly, the higher the average $[CH_3Hg^+]_{liver}/[CH_3Hg^+]_{muscle}$ ratio of a fish species, the weaker the tendency of that species to accumulate CH_3Hg^+ from its environment; thus, whitefish have an anomalously weak affinity for environmental CH_3Hg^+. It is also worth noting that the lower limit of the range of values for the CH_3Hg^+/total Hg ratio of muscle tissue was much lower for whitefish than for walleye or pike at each of the four sampling sites, and the same was true of liver tissue at three of the sites (Table 3). The results of the study appear to contradict the findings of Jernelöv and Lann (1971), who concluded that higher values of the $[CH_3Hg^+]_{liver}/[CH_3Hg^+]_{muscle}$ ratio (~1) imply that the CH_3Hg^+ concentrations in the fish are increasing whereas lower values (~0.5) imply that they are decreasing.

The results are tentatively interpreted as follows. CH_3Hg^+, being somewhat lipophilic, besides being subject to strong binding by sulfhydryl groups of proteins, is readily absorbed and retained by fish tissues and is not readily excreted (Huckabee et al. 1979); but in whitefish, CH_3Hg^+ may be bonded to water-soluble "carrier" molecules to form hydrophilic, and therefore readily excreted, complexes (compare Jernelöv and Lann 1971; Norseth and Clarkson 1971; Ruohtula and Miettinen 1975; Ariëns et al. 1976; Farris et al. 1977). The anomalously high $[CH_3Hg^+]_{liver}/[CH_3Hg^+]_{muscle}$ ratio of whitefish is particularly suggestive in this regard. The biochemical compounds that seem best suited to function as carriers include various thiols, the amino acid cysteine, and sulfur-bearing peptides and proteins, as such compounds are able to bind CH_3Hg^+ by means of dissociated sulfhydryl groups ($-S^-$). Another possibility is that CH_3Hg^+ is broken down by demethylation in certain organs such as the liver before it reaches the muscle — or is demethylated in the muscle itself — after which the resulting inorganic Hg is eliminated with the assistance of carrier molecules (Norseth and Clarkson 1970, 1971; Burrows and Krenkel 1973). The high $[CH_3Hg^+]_{liver}/[CH_3Hg^+]_{muscle}$ ratio appears to militate against an important role for demethylation in the liver but is consistent with the possibility of demethylation in the muscle. However, we must not overlook the hypothetical possibility that the "CH_3Hg^+" fraction of the liver actually included some elemental mercury (Hg^0) generated by demethylation: Hg^0, like CH_3Hg^+, is somewhat lipophilic (Gavis and Ferguson 1972), and it will be recalled that the method used for determination of CH_3Hg^+ in fish tissues does not differentiate between CH_3Hg^+ and other lipophilic Hg species.

It is also conceivable that water-soluble CH_3Hg^+ complexes are formed by the benthic invertebrates on which the whitefish feed and that these complexes are ingested and subsequently excreted by the fish. This could be the common denominator which explains why both benthic invertebrates and whitefish have such a low affinity for environmental CH_3Hg^+ — especially in view of the evidence suggesting that most of the CH_3Hg^+ taken up by whitefish is absorbed from the water instead of being ingested with food (see above).

Clearly there is scope for more research on the biochemical and physiological causes of the poorly developed ability of certain organisms such as whitefish and benthic invertebrates to accumulate CH_3Hg^+. The data and tentative interpretations presented here suggest some avenues of future investigation which may be worth pursuing.

Acknowledgments

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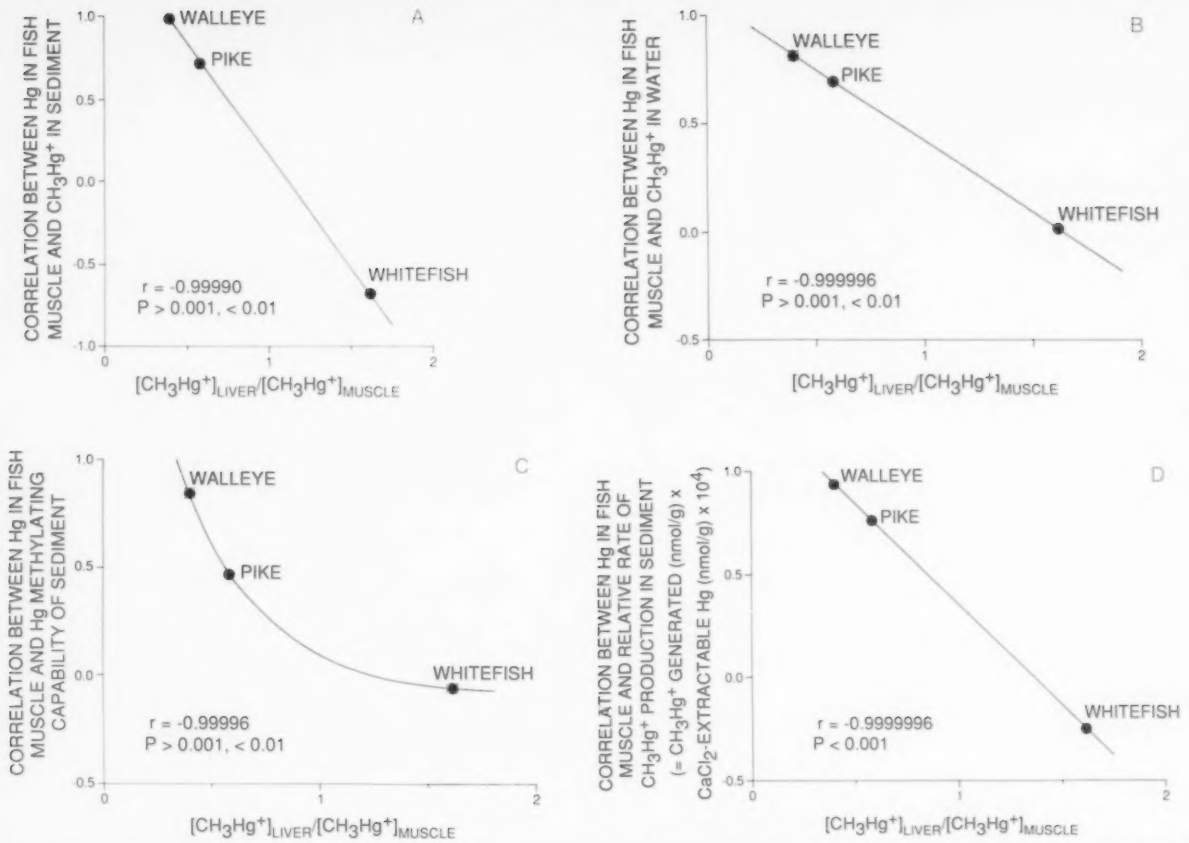

FIG. 16. Correlation coefficients relating the Hg content of walleye, northern pike, and lake whitefish muscle to the (A) CH_3Hg^+ content of the sediment, (B) CH_3Hg^+ content of centrifuged surface water, (C) Hg methylating capability of the sediment, and (D) relative rate of CH_3Hg^+ production in the sediment ("Hg methylating capability" × $CaCl_2$-extractable Hg content) plotted against the ratio of the CH_3Hg^+ content of the liver of the fish to the CH_3Hg^+ content of its muscle. Values on the *y*-axis represent fish collected from Southern Indian Lake and Notigi Reservoir lakes in 1980; values on the *x*-axis represent fish collected from four regions of Southern Indian Lake in 1980. Dates of sediment sample collection: samples analysed for CH_3Hg^+, June 1981; samples analysed for $CaCl_2$-extractable Hg and water analysed for CH_3Hg^+, June and August 1981; sediments analysed for Hg methylating capability, August 1983.

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Lactation in the Ringed Seal (*Phoca hispida*)

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Length of lactation, pup growth rate, and female weight loss in ringed seals (*Phoca hispida*) were estimated using cross-sectional data from the Canadian and Norwegian Arctic. At birth the pups had a standard length of 63.4 cm (SE = 1.3, N = 11) and weighed 5.4 kg (SE = 0.4, N = 6). Weaning occurred approximately 39 d (range 36–41 d) after birth at an estimated length of 88.4 cm (SE = 0.65, N = 96) and an estimated weight of 22.1 kg, resulting in an increase in length of 0.64 cm·d^{-1} and a weight change of 0.43 kg·d^{-1}. Regression of female weight on the number of days after the nominal date of birth for each region indicated that the postpartum female weighed 81.2 kg and lost 0.64 kg·d^{-1} (95% CI = ±0.20). During lactation, female weight declined by an estimated 32%, with much of the loss occurring from the blubber. Analyses of stomachs indicated that ringed seals supplemented stored energy reserves by feeding during lactation.

La durée de la lactation, le taux de croissance des jeunes et la perte de poids des phoques annelés (*Phoca hispida*) femelles ont été estimés à partir des données recueillies dans l'arctique canadien et norvégien. A la naissance, les jeunes phoques mesuraient en moyenne 63.4 cm (ET = 1,3, N = 11) et pesaient 5,4 kg (ET = 0,4, N = 6). Les jeunes sont sevrés approximativement à 39 jours (entre 36 et 41 jours) après la naissance et ils mesurent alors environ 88,4 cm (ET = 0,65, N = 96) tandis qu'ils pèsent 22,1 kg, ce qui correspond à un accroissement de taille de 0,64 cm par jour et une variation de masse de 0,43 kg par jour. La diminution du poids des femelles en fonction du nombre de jours nécessaire pour sevrer les jeunes après leur naissance dénombre que les femelles au début de la période de lactation pèsent 81,2 kg et perdent 0,64 kg par jour (95 % IC = ±0,20). Durant la lactation, le poids des femelles qui allaitent décroît d'environ 32 % avec une perte plus importante au niveau des graisses. Les analyses stomacales indiquent que chez les phoques annelés femelles, des réserves énergétiques compensatoires sont emmagasinées au moyen d'une nutrition durant l'allaitement des jeunes.

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Lactation represents a major parental investment requiring three times more energy than gestation (Millar 1977) and for some pinnipeds a sixfold increase in daily energy output compared with normal maintenance requirements (Fedak and Anderson 1982). In otariids, lactation is characterized by alternating nursing bouts and active foraging trips, during which the female leaves the pup unattended for several days. Pup growth is slow and lactation lasts for up to 12 mo (Oftedal et al. 1987). The general phocid lactation strategy is quite different; the females fast, often losing 16–46% of their initial body weight (Fedak and Anderson 1982; Stewart and Lavigne 1984; Bowen et al. 1987; Tedman and Green 1987; Kovacs et al. 1991). Pup growth is rapid and lactation is of short duration (4–60 d) (Oftedal et al. 1987).

The ringed seal (*Phoca hispida*) is one of the smallest pinnipeds (King 1983). It is circumpolar in distribution, occupying both fast-ice and pack-ice covered waters (McLaren 1958; Finley et al. 1983). Throughout much of their range, the pups are born inside subnivean lairs, which provide shelter from cold temperatures and predators (McLaren 1958; Smith and Stirling 1975; Smith 1976, 1980; Stirling and Archibald 1977; Lydersen and Smith 1989).

Unlike most other pinnpeds, direct observation of maternal behaviour is not possible because both the female and her pup are hidden inside the lair. Ringed seals have also evolved under intense predation pressure (Hammill and Smith 1991). Consequently, they are sensitive to noise from the surface (Burns and Kelly 1982) and the females will move the pup to alternate lairs or completely abandon structures (Smith 1987) when disturbed. Owing to these difficulties, little is known about the biology of lactation in this species. Lactation is thought to last for 38–60 d, which would make it the longest of any phocid (McLaren 1958; Smith 1987). Based on small samples, pup growth rate has been estimated as 0.45–0.76 kg·d^{-1}, while females lose an estimated 0.16–0.45–kg·d^{-1} (Smith 1987; Ryg et al. 1990; Smith et al. 1991).

The subject of lactation in the ringed seal has only been dealt with in the context of the general reproductive cycle (McLaren 1958; Smith 1973, 1987; Lydersen and Gjertz 1987). Here, we combine data from the Canadian arctic and Spitzbergen (west-

TABLE 1. Number of pregnant and lactating ringed seal females collected early in the pupping season from Barrow Strait, Northwest Territories, and from Svalbard.

Date	Number of pregnant females	Number of lactating females
	Barrow Strait	
22–31 March	2	0
1–10 April	2	1
11–20 April	2	0
21–30 April	0	2
1–10 May	—	—
11–20 May	0	7
21–30 May	0	9
	Svalbard	
1–10 April	2	6
11–20 April	1	2
21–30 April	0	5

ern Svalbard) to examine duration of lactation, pup growth, and female weight loss.

Materials and Methods

Ringed seal specimens were killed by native hunters or under permit (Norway), using a high-powered rifle, in breathing holes or lairs or after they had hauled out on the ice in Barrow Strait (74°N, 94°W) during 1984–86 (48 females, 21 pups), in Amundsen gulf (70°N, 117°W) during 1971–83 (44 females, 72 pups) (Smith 1987), off eastern Baffin Island (67°N, 63°W) in 1967–68 (3 females, 32 pups), off southeastern Baffin Island (64°N, 65°W) in 1979 (3 females, 8 pups), and at Svalbard (78°N, 9°E) during 1981–90 (28 females, 19 pups).

Morphometric measurements included standard length measured to the nearest 0.5 cm (American Society of Mammalogists 1967) and body weight and sculp weight weighed to the nearest 0.2 kg. The sculp consisting of skin with attached blubber was dissected from the body between the external ear openings and the base of the hind flippers. Body weight was not corrected for loss of fluids. Many of the samples were incomplete. Standard length was measured in most cases, but few of the early samples obtained body weight or sculp weight, resulting in unequal sample sizes in our analyses.

Females were examined for evidence of lactation by mammary incision. those animals with a grey or clear discharge were considered to have been lactating, but the pup had recently been weaned or lost to a predator. Female reproductive tracts were removed and preserved in 10% formalin. Ovaries were sectioned by hand and examined visually for the presence of follicles >5 mm and active corpora lutea (Smith 1973).

The mean date of ovulation and end of lactation were estimated by transforming the proportion of ovulating females and proportion of females which had finished lactation, respectively, to probits and regressing these against the log date of sampling (Caughley 1977).

Stomachs were removed and the contents preserved in 10% formalin. Stomach contents were identified where possible to species.

Differences between means and weight loss regressions were determined using Proc GLM and Proc REG of the Statistical Analysis System (SAS Institute Inc. 1987).

TABLE 2. Number of female ringed seals that have ovulated or finished lactation at the time of sampling from Barrow Strait and Svalbard.

Date	Number of females	Percent ovulated	Number of females	Percent finished lactation
		Barrow Strait		
11–16 May	1	0	2	0
17–22 May	6	0	8	38
23–28 May	9	22	8	50
29–3 June	6	67	6	50
4–9 June	8	75	7	57
10–15 June	12	75	10	60
16–21 June	14	79	11	64
22–27 June	1	100		
		Svalbard		
11–20 April	7	14	8	12
21–30 April	10	20	8	12
1–10 May	8	33	11	36
11–20 May	8	62	7	57
21–30 May	3	33	2	50
31–9 June	3	67	3	67
10–20 June	4	75	3	67

Results and Discussion

Pups

In Canada, peak pupping occurs at the beginning of April on southeastern and eastern Baffin Island (McLaren 1958; Smith 1973) and 15 April in the Amundsen Gulf area (Smith 1987). In Barrow Strait, we surveyed the breeding habitat using trained dogs to locate the subnivean structures of the ringed seal beginning in mid-March, but the first birth lairs were not detected until 4 April (Hammill and Smith 1989). A lactating female was collected as early as 3 April 1984, and the last pregnant female was collected 19 April. In a small sample of 25 females the mean date of pupping would appear to occur around 20 April (Table 1). An alternative estimate can be derived from the approximate dates of birth of three neonates. These pups were collected on 27 April, 8 May, and 16 April and had standard lengths of 60.5, 66, and 60 cm, respectively, which did not differ significantly from the standard lengths of four late-term fetuses ($\bar{x}$ = 62.2 cm, SE = 1.2), indicating recent birth. The mean date of birth for these pups would be 27 April (SE = 6.4), a few days later than the above estimate.

On Svalbard, the snow covering the lair is often quite thin and very soft and the pups may be observed exposed on the ice. Pups have been collected as early as 24 March and pregnant females as late as 14 April. In spite of its northern latitude (78°N), peak pupping occurs in this area in early April (Table 1).

In Barrow Strait, a pup with milk in its stomach was collected 10 June and a lactating female was collected 18 June 1986, the last day of hunting in that year. The mean date for the end of lactation based on the proportion of females, which had finished lactation in May and June, was 27 May (Probit percent nonlactating females = 3.97 + 0.86 · (log date); $F_{1,6} = 94.4$, $p < 0.0006$, $r^2 = 0.96$) (Table 2), indicating a lactation period of 37 d if the nominal birth date is 20 April. The mean date of ovulation based on the proportion of reproductive tracts collected after 20 April, with an active corpus luteum or follicle

>5 mm, was estimated as 29 May (Probit percent females ovulated = 2.49 + 2.35 · (log date); $F_{1,6} = 17$, $p < 0.03$, $r^2 = 0.85$) (Table 2). If ovulation occurs around the time of weaning, then the minimum lactation period is 39 d.

On Svalbard, a lactating female was collected as late as 13 June. The mean date of weaning based on the proportion of females that had ovulated was 14 May (Probit percent females ovulated = 3.68 + 0.87 · (log date); $F_{1,7} = 9.2$, $p < 0.03$, $r^2 = 0.65$) (Table 2). If the proportion of females that had finished lactation is used, then the mean date for weaning is 14 May (Probit percent nonlactating females = 3.53 + 0.97·(log date): $F_{1,7} = 13.9$, $p < 0.01$, $r^2 = 0.74$) (Table 2), resulting in a lactation period of 39 d for the Svalbard area, if the nominal date of birth is 5 April.

In Amundsen Gulf, Smith (1987) found milk in a small sample of pups up to 38 d after the nominal birth date of 15 April. The mean date of ovulation in Amundsen Gulf is 21 May, giving a lactation period of 36 d (Smith 1987). It is likely that we have underestimated the duration of lactation using the date of ovulation to indicate weaning. Assuming a lag of 2 d between ovulation and weaning (Boness and James 1979) for the estimates of duration of lactation based on mean date of ovulation and averaging the estimates from the different regions results in a mean length of lactation of 39 d (SE = 0.7, N = 6).

The subnivean lair interferes with attempts to determine size at birth. Three pups were captured on Svalbard still covered in amniotic fluid, indicating recent birth. Mean length was 62 cm (SE = 0.6) and mean weight was 4.6 kg (SE = 0.6). We also examined the combined data from all areas using only fetuses or neonates collected within 7 d of the nominal date of birth for each area. The mean length of the late term fetuses was 62.2 cm (SE = 1.2, N = 4) and the mean weight was 5.8 kg (SE = 0.4, N = 2). The neonates had an average length of 64.1 cm (SE = 2.0, N = 7) and weighed 5.4 kg (SE = 0.4, N = 6). No significant differences were seen between the two groups. Pooling of the data resulted in a mean length at birth of 63.4 cm (SE = 1.3, N = 11) and a mean weight of 5.4 kg (SE = 0.3, N = 8). The pups are born with very little subcutaneous blubber. The mean weight of fat dissected from the skin of five late-term fetuses and neonates was 310 g (SE = 60.4).

After several weeks the white lanugo is shed. The hair of the moulted pelt is somewhat longer than the adult pelage and the pups at this stage are referred to as silver jars (McLaren 1958). Late in the spring the subnivean lairs begin to melt open and it is sometimes possible to observe the pups on the ice by themselves or beside the female. At the time of weaning, pups with an estimated age of >36 d attained a mean length of 88.4 cm (SE = 0.65, N = 96, range 73–101) and weighed 18.7 kg (SE = 0.75, N = 59, range 9.1–33.2). Because we were unable to determine the exact date of weaning, it is likely that we underestimated the weaning weight of the pup. At the time of weaning, the pup's weight will have attained a maximum. To determine weight at weaning, we regressed log body weight on log standard length of pups with an estimated age of less than 40 d (Fig. 1). This resulted in an estimated weaning weight of 22.1 kg for an 88.4-cm pup. If lactation lasts for 39 d, then ringed seal pups gain weight at a rate of 0.43 kg·d^{-1} and increase in length at a rate of 0.64 cm·d^{-1}. Pup growth is associated with considerable blubber deposition. In four animals from Barrow Strait, the sculp formed 47% of the total body weight (mean sculp weight = 10.4 kg, SE = 0.5).

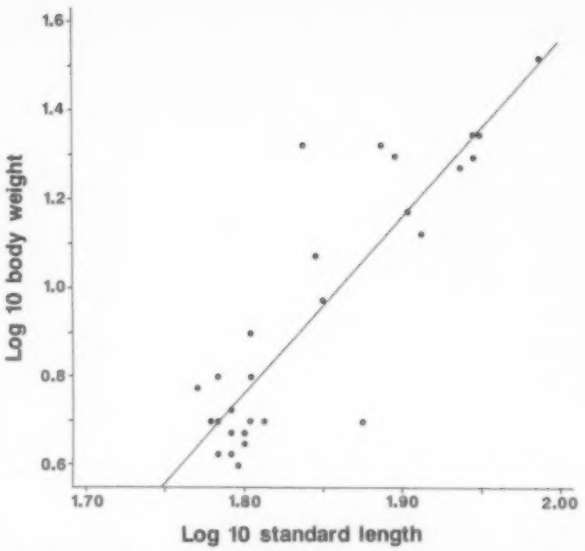

FIG. 1. Weight–length relationships for lactating ringed seal pups. The solid line represents the equation log body weight (kg) = 4.02·log standard length (cm) − 6.47 ($F_{1,30} = 103$, $p < 0.01$, $s_{yx} = 0.39$, $r^2 = 0.79$).

Adults

Female weight loss during lactation could be described by the regression equation body weight (kg) = 77.6 − 0.44·(days), ($F = 47.1$, df = 1,110 $r^2 = 0.30$) where days is the number of days after the nominal pupping date that the female was collected. In ringed seals the season of births may last for over a month (Smith 1987), and in our samples two lactating females from Amundsen Gulf were killed 78 d after the mean pupping date. If the exact stage of lactation is not known, and if larger females give birth earlier in the season than do smaller females, then the cross-sectional approach may underestimate the rate of female weight loss (Anderson and Fedak 1987). Ryg et al. (1990) found a decrease in standard lengths of mature females collected between late March and late May, suggesting that larger females do give birth earlier in the season than do smaller females. We attempted to correct for this by excluding females still lactating very late in the spring. Since lactation lasts for up to 41 d, we excluded any lactating female collected ≥50 d after the mean pupping date in each region. Using this approach, females were estimated to lose 0.64 kg · d^{-1} (95% CI = ±0.20 kg) during lactation (Fig. 2). The regression of sculp weight on number of days after the nominal date of birth, sculp weight (kg) = 40.7 − 0.43 · (days) ($F_{1,40} = 48.9$, $p > 0.0001$, $r^2 = 0.50$), was significant. The regression of lean carcass weight, calculated by subtracting sculp weight from total body weight, was not significant ($F_{1,40} = 1.5$, $p > 0.3$), indicating that the loss in weight by the female occurred primarily from the sculp.

Stomach Contents

Food remains were found in 37% (N = 27) of stomachs of lactating females from Barrow Strait. Eight stomachs contained only fish remains, mainly Arctic food (*Boreogadus saida*). A squid beak (*Rossia* sp.) was found in one stomach, one stomach contained only zooplankton remains, and another contained

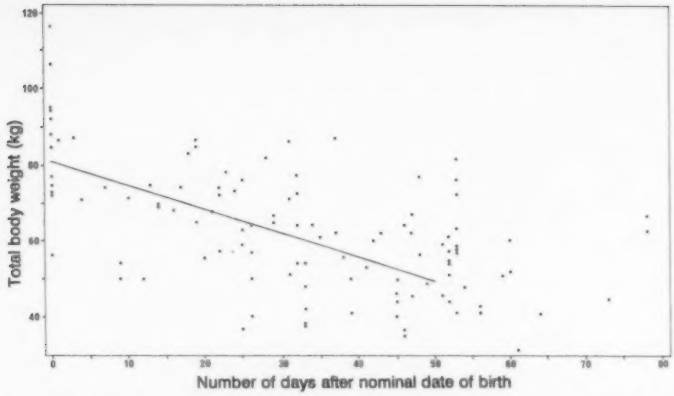

FIG. 2. Body weight of lactating female ringed seals collected on different days after the nominal date of birth. The solid line represents the equation female body weight (kg) = 81.2 − 0.64·(days) ($F_{1,80} = 42.3$, $p < 0.0001$, $s_{yx} = 0.098$, $r^2 = 0.35$).

TABLE 3. Summary of female weight loss and pup weight gain amongst phocids (modified after Bowen et al. 1987).

Species	Initial female weight (kg)	Weight loss (kg)	Weight loss (%)	Fraction of fat store (%)	Pup weight gain/ female weight loss (%)	Lactation period (d)	Source
Grey seal	170	65	38	84	46	18	Fedak and Anderson 1982
Harp seal	139	39	28	—	77	13	Kovacs et al. 1991[a]
					65		Kovacs et al. 1991[b]
	129	29	22	44	88		Stewart and Lavigne 1984[b]
Weddell seal	447	205	46	—	44	45	Tedman and Green 1987
	376				48		Testa et al. 1989
Hawaiian Monk seal	261	88	34	—	51	35	Kenyon and Rice 1959
Northern elephant seal	504	157	31	58	55	26	Costa et al. 1986[a]
Hooded seal	179	29	16	33	76	4	Bowen et al. 1987[b]
Ringed seal	81	26	32	74	67	39	This study[b]

[a]Longitudinal data.
[b]Cross-sectional data.

both zooplankton and fish. Food remains consisting primarily of Arctic cod otoliths were observed in 57% ($N = 23$) of the stomachs and intestines examined from Svalbard (Gjertz and Lydersen 1986). Fifty-one percent of stomachs ($N = 37$) from Amundsen Gulf contained food. Four of 19 stomachs contained squid beaks, and 7 of 19 stomachs contained Arctic cod remains. Stomach contents were not identified in the remaining eight stomachs.

Energy Budget

A distinguishing feature of the energy budget in phocids has been the reduction in length of the lactation period. In a fasting animal, this results in fewer days spent using stored energy reserves to satisfy maintenance requirements (Fedak and Anderson 1982). The shortest lactation periods, probably influenced by the instability of their pupping habitat, are observed in the pack-ice species, the hooded seal (*Cystophora cristata*) and the harp seal (*Phoca groenlandica*), with lactation periods of 4 and 12 d, respectively (Bowen et al. 1987; Kovacs and Lavigne 1985). The longest lactation periods are observed in fast-ice species, the ringed seal (39 d) and Weddell seal (*Leptonychotes weddelli*) (45 d; Tedman and Green 1987), while lactation in terrestrial breeding phocids is intermediate in length ($\bar{x} = 30.5$ d) (Oftedal et al. 1987).

We observed a wide range in weights of apparently weaned pups. Part of this variability may be due to the relatively easy detection and capture of abandoned pups. However, in some areas, intense predation pressure from arctic foxes and polar bears may remove up to 44% of the estimated pup production during the lactation period (Smith 1987; Hammill and Smith 1991). Variability in disturbance from predators may affect growth during lactation. To avoid predators the pups are moved underwater by the female or they swim under the ice to alternate breathing holes (M. O. Hammill, C. Lydersen, M. Ryg, and T. G. Smith, pers. obs.). Predator activity will not only interrupt the normal suckling pattern, but immersion in water before deposition of sufficient blubber and higher activity levels may result in increased energy expenditure for maintenance (Smith et al. 1991) rather than growth.

In most phocids, energy required for maintenance and milk production is supplied by the conversion of stored reserves (Oftedal et al. 1987). Other studies have documented a wide range in utilization of fat stores, which may be related to length of lactation, female size, activity, and fat content of the milk (Bowen et al. 1987) (Table 3). At the start of lactation, the postpartum female ringed seal weighs 81.2 kg, which can be partitioned into 40.5 kg in the sculp and 40.7 kg in the core. Skin weight is related to standard length: skin weight (g) =

standard length (cm)$^{1.75}$ (Hammill 1987). In an adult female with an asymptotic length of 128 cm (Lydersen and Gjertz 1987), the skin would weigh 4.9 kg. Subtracting skin weight from the sculp gives a total blubber weight of 35.6 kg. Assuming that the fat content of the blubber is 94% (Worthy and Lavigne 1983) and the core is 5% fat (Hammill 1987), then the total fat reserve in the postpartum female would be 35.5 kg representing 44% of her total body weight. During lactation, female ringed seals lose 26 kg (0.64 kg·d^{-1}) or 32% of their initial body weight. If the weight loss consists entirely of fat, then she will utilize 74% of her stored fat reserves (Table 3).

The ratio of pup weight gain to female weight loss provides an indication of efficiency of weight transfer between the female and pup. The highest efficiencies of weight transfer are seen among the pack-ice species, the hooded and harp seal (Bowen et al. 1987; Stewart and Lavigne 1984; Kovacs et al. 1991), while the fast-ice breeding Weddell seal and terrestrial breeding grey seal are among the lowest (Table 3). The ringed seal reproduces in the fast-ice, has a long lactation, and a very slowly growing pup. We would expect the efficiency of weight transfer in this species to be similar to that of the Weddell seal, its ecological, but much larger counterpart in the Antarctic (Table 3). However, our data indicate an efficiency of weight transfer of 67%, which is even higher than the rate of 55% observed in the much larger northern elephant seal (*Mirounga augustirostris*) (Costa et al. 1986) (Table 3).

This high efficiency of weight transfer may result from errors associated with our sampling procedure. The difficulties in making direct observations on female–pup weight changes during lactation and their prolonged pupping season, combined with our inability to determine the stage of lactation in suckling pups and lactating females, may have led to an underestimation of the rate of female weight loss, or an overestimation of the rate of pup weight gain.

An alternative explanation for the estimated high efficiency of weight transfer is that females are supplementing stored fat reserves by feeding under the ice during the lactation period. Although our stomach content data support this hypothesis, we have not been able to quantify food consumption during the lactation period. Ryg et al. (1990) reported reduced feeding during the spring, but ringed seals feed most actively between 18:00 and 24:00 (Smith 1987), while sampling during the lactation period typically occurs between 10:00 and 16:00, after stomach contents have been digested (Murie and Lavigne 1985). Lydersen (1991) found that a lactating female spent 55% of her time in the water, primarily between 20:00 and 01:00, and 70% of this time was spent diving, suggesting that the animal was actively foraging beneath the ice.

Feeding has been reported in lactating harp seals, but appears to be opportunistic (Stewart and Murie 1986). Feeding by lactating Weddell seals has been suggested and may be important, especially for smaller, younger females for whom the costs of lactation would be relatively greater than for older, larger individuals (Siniff et al. 1977; Testa et al. 1985; Testa et al. 1989; Stewart 1986).

If without feeding, the efficiency of weight transfer in ringed seals was similar to that of the Weddell seal (48%) (Table 3), then females would lose 0.90 kg·d^{-1}. At this rate, females would lose 35 kg during lactation and utilize 99% of their stored fat reserves. This is much higher than has been reported for other species (Table 3) and would leave the female ringed seal with too little blubber for thermoregulation.

The use of weight transfer to determine the energetic costs of lactation is based on the assumptions that females fast during lactation and that the pups derive all of their energy requirements from their mother (Testa et al. 1989). For the majority of the large phocids, these assumptions appear to be true. Few studies have examined weight transfer in smaller phocids. The small size of the ringed seal may place an upper limit on stored energy reserves. This coupled with the long nurturing period and the slow growth of the pup indicates that access to food resources under the ice may form an important component of the ringed seal lactation strategy.

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Biotic Responses along the Recovery Gradient of a Regulated Stream

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Voelz, N. J., and J. V. Ward. 1991. Biotic responses along the recovery gradient of a regulated stream. Can. J. Fish. Aquat. Sci. 48: 2477–2490.

Samples were collected year-round over a 1-yr period at six sites located downstream from a reservoir with a hypolimnetic release on the upper Colorado River to examine the longitudinal patterns of macroinvertebrates along an environmental gradient induced by river regulation. The impoundment had only minimal effects on river chemistry, and chemical variables did not exhibit a distinct downstream gradient. Macroinvertebrate density was highest at sites near the Granby Reservoir dam, but diversity increased with distance from the impoundment. A percentage similarity matrix identified two areas of rapid transition in macroinvertebrate assemblages along the regulated river gradient. Detrended correspondence analyses (DCA) showed a sequential faunal gradient with the most rapid change occurring within the first 3.0 km below the impoundment. Detrended canonical correspondence analysis (DCCA) suggested that downstream decreases in periphyton standing crop and minimum temperatures and downstream increases in most food resources and maximum temperatures were major variables structuring faunal assemblages. The results of this study, when compared with research conducted in free-flowing and other impounded rivers, indicated the predictability of some longitudinal patterns and the recovery potential of regulated lotic systems.

Des échantillons ont été prélevés pendant toute une année en six endroits situés en aval d'un réservoir à décharge hypolimnétique sur le cours supérieur du Colorado, dans le but d'examiner les tendances longitudinales des macroinvertébrés le long d'un gradient envirionnemental dû à la régularisation du cours d'eau. Le réservoir n'a eu que des effets minimes sur la chimie du cours d'eau, et les variables chimiques n'ont présenté aucun gradient distinct en aval. La densité de macrovertébrés était la plus forte aux endroits proches du barrage de Granby Reservoir, mais la diversité augmente en s'éloignant du réservoir. Une matrice de pourcentages de similarité a permis de repérer deux zones de transition rapide dans les assemblages de macroinvertébrés le long du gradient du cours régularisé. Des analyses de correspondances décomposées ont révélé la présence d'un gradient faunistique séquentiel avec la variation la plus forte se produisant dans les 3,0 premiers km en aval du réservoir. Une analyse de correspondances canoniques décomposées a indiqué que les principales variables de structure des assemblages faunistiques étaient les diminutions en aval de la biomasse de périphyton et des températures minimales, ainsi que les augmentations en aval de la pluparts des ressources de nourriture et des températures maximales. les résultats de cette étude, une fois comparées à celles de la recherche menée des eaux vives et d'autres réservoirs, ont montré que certaines tendances longitudinales étaient prévisibles et que les systèmes lotiques régularisés pouvaient être rétablis.

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Stream biologists have long invoked physical processes as having primary structuring influence on lotic macroinvertebrate assemblages (Percival and Whitehead 1929; Pennak and Van Gerpen 1947; Cummins and Lauff 1969; Allan 1975; Vannote and Sweeney 1980; Frissell et al. 1986). Some stream research has examined the potential role of biotic interactions as structuring forces. Both competition (Hart 1983; McAuliffe 1984) and predation (Peckarsky and Dodson 1980; Cooper 1988) have received increased attention. Power et al. (1988) have emphasized the complexity of biotic and abiotic interactions in stream ecosystems. Recently, streamflow variability has been implicated as a major factor influencing the relative importance of abiotic and biotic factors in regulating lotic community processes and patterns (Poff and Ward 1989).

Identifying the distributional patterns of species is an important first step in determining what processes may control the structure of riverine communities. Species respond uniquely along environmental gradients (Whittaker 1967; Ter Braak and Prentice 1988) at various levels of spatial resolution (e.g. from headwaters to river mouths; across the surfaces of individual rocks). The heuristic value of descriptive gradient analyses cannot be overestimated, as many hypotheses can be generated for experimental (mechanistic) testing. Regulated rivers are especially suited for such endeavors because environmental changes that may take hundreds of kilometres to develop in free-flowing rivers are compressed into tens of kilometres (Ward and Stanford 1984).

The downstream changes in the biotic and abiotic character of rivers influenced by regulation are numerous and complex (e.g. Peñáz et al. 1968; Ward 1982; Armitage 1984; Petts 1984). For example, decreased thermal heterogeneity, a dampening of flow fluctuations, truncation of suspended material,

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and increased algal growth, among other modifications, can occur in streams below deep-release impoundments. The faunal community often responds in unique ways to these alterations. Few studies have examined the changes in both environmental factors and macroinvertebrates at several sites along a regulated river gradient (Peñáz et al. 1968; Lehmkuhl 1972; Ward 1974; Voelz and Ward 1989, 1990).

This study was designed to examine downstream changes in environmental conditions in an attempt to identify processes that may be responsible for lotic macroinvertebrate patterns in a regulated river located in the Colorado Rocky Mountains. Three questions were asked in this study: (1) Are there predictable downstream patterns in species abundance and diversity? (2) Do environmental variables exhibit discernible patterns with progressive distance downstream of the impoundment? and (3) If they exist, are there any distinct relationships between the biotic and environmental gradients? We began our examination of patterns by comparing some direct longitudinal relationships between environmental variables and the distribution of macroinvertebrates. More complex methods for examining pattern were then tested, first using the macroinvertebrate data alone and then by using an analysis that simultaneously compared macroinvertebrate data and the environmental variables.

Methods

Site Description

The Colorado River drains one twelfth of the United States and is fed by snowmelt from the western slope of the southern Rocky Mountains (Stanford and Ward 1986). The Colorado River below Granby Reservoir (Fig. 1) is a sixth-order, high-gradient stream. Granby Reservoir (40°11′N, 105°52′W), a large (91-m-high dam, 666 × 10^6 m^3 capacity), deep-release storage impoundment, was constructed in the 1940s as part of the Colorado – Big Thompson interbasin transfer project. This scheme was implemented to divert a portion of the discharge of the Colorado River (and some downstream tributaries) through the Continental Divide, via a 21-km tunnel, to the South Platte River basin on the eastern slope of Colorado (Pennak 1963).

Six sampling sites were established in riffles downstream of the dam using approximately a geometric progression starting at 0.25 km (Fig. 1, bottom). Maximum depth in all riffles was <1 m. Two small tributaries enter the river between the dam and site C4. They did not contribute measurably to river discharge. An additional tributary, Willow Creek, enters the river between sites C5 and C6, approximately 5 km upstream from site C6 (Fig. 1). This tributary is part of the interbasin transfer scheme and is regulated by Willow Creek Reservoir, which is located approximately 6 km upstream from the confluence of Willow Creek with the Colorado River. Water is diverted from Willow Creek Reservoir to Granby Reservoir. Data for most variables were collected monthly (November 1984 – October 1985), except when high flows precluded sampling at site C6 during May. Information for variables sampled seasonally was obtained during January, April, July, and October 1985.

Physical and Chemical Variables

Most chemical variables were measured monthly in the field. Dissolved O_2 was determined using the azide modification of the Winkler method. The pH was measured with Hellige color discs. Total hardness was assessed with a Hach titration method (using Man Ver2 hardness reagent) and bound CO_2 (methyl orange alkalinity) was measured with methyl orange and HCl titration (Pennak 1977). Water samples for nitrate-nitrogen were brought bank to the laboratory and examined with the Hach cadmium reduction method and a spectrophotometer. Total dissolved solids were determined seasonally by filtration and subsequent evaporation of 1-L water samples (Ward 1974).

A composite mineral substratum sample was taken seasonally at each site using a metal core that enclosed an area of 479.2 cm^2 (diameter = 24.7 cm). Mass of the cobble and pebble fractions was determined in the field by displacement, with subsequent conversion using specific densities. A subsample of the smaller substratum was brought back to the laboratory, wet-sieved into different size categories, and dried to constant mass at 60°C.

When possible, water temperature was recorded with precalibrated maximum–minimum thermometers. Spot temperatures were taken monthly at each site. Discharge data were obtained from U.S. Geological Survey records. Gauging stations were located near sites C2 and C5 (0.5 and 4.8 km, respectively, below Granby Reservoir). In addition, Willow Creek flow records were used to estimate total discharge at site C6.

Food Resource and Macroinvertebrate Samples

Periphyton samples were taken monthly using a template to scrape 40.7 cm^2 of the top surfaces of each of three rocks per site with a scalpel. Periphyton samples were preserved in the field with 5% formalin. Samples were dried to constant mass at 60°C and fired in a muffle furnace for 24 h at 550°C to obtain ash-free dry mass (AFDM).

Three sedimentary detritus samples were taken seasonally per site with the metal coring device (479.2 cm^2). A measuring tape, placed on the stream bank, was used to randomly determine a stepping-off point for sample locations. Sampling was started 1–3 m from the stream bank, depending on the site, to ensure that all samples were collected in perennially wetted areas. A structured random sampling procedure was used to reduce hydrological variability within and between sites. Samples were collected 1.0–1.5 m apart, in a roughly square configuration. Average current velocity (6/10 depth) was measured (during different flow regimes) at each site in the middle of the sample cluster using a pygmy Gurley meter. For each sample, the core was driven 4–10 cm into the substratum and cobble-sized rocks were scrubbed by hand and removed. The substratum remaining within the core was agitated and water containing suspended matter was pumped into a bucket with a hand pump (Guzzler 500, United States Plastics Corporation, Lima, OH). Water and detritus from the bucket were passed through 1000- and 75-μm sieves. Sampling continued until the water in the core began to clear (approximately 30–60 L). Detritus samples were preserved in the field with 5% formalin.

The >1000 μm detritus fraction (coarse particulate organic matter, CPOM) was further divided in the laboratory into four categories: conifer needles, deciduous leaves, wood, and other material (e.g. grass, roots, buds). Algae and bryophytes were removed from the samples and discarded. The 75–1000 μm detritus fraction (fine particulate organic matter, FPOM) was divided in the laboratory into 75–250 and 250–1000 μm com-

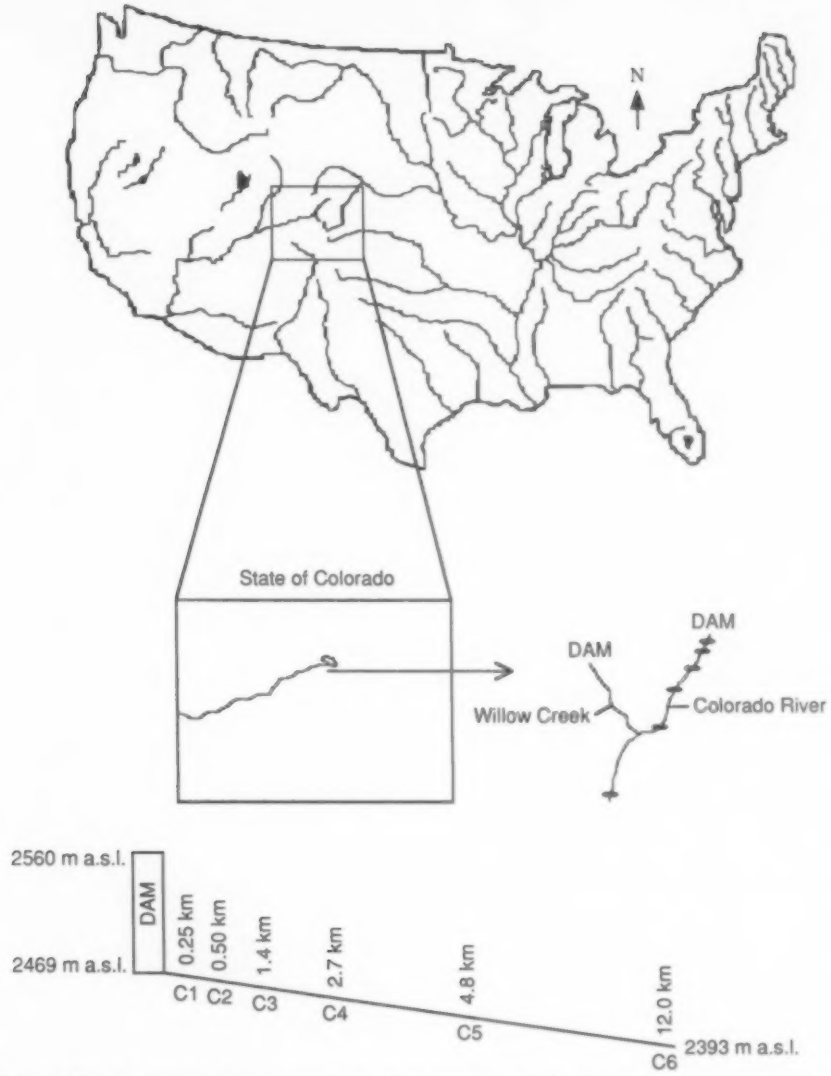


FIG. 1. Map of the major river systems in the United States with the State of Colorado outlined. The Colorado River below Granby Reservoir is shown. Locations of sampling sites (C1–C6) are shown diagrammatically (bottom).

ponents. AFDM for CPOM and FPOM was determined as for periphyton.

Total suspended organic matter (organic seston) was assessed by drying (60°C) the filtrate (0.45-μm Millipore filters) from the total dissolved solids analysis and determining loss-on-ignition (550°C).

Four benthic macroinvertebrate samples were collected monthly per site using the metal core. Location of samples was determined as outlined above. The core was driven into the substratum as described for sedimentary detritus samples, and large rocks were transferred to a bucket containing water. This larger substratum was hand-scrubbed and visually examined before returning it to the stream. The water and invertebrates remaining in the bucket were poured through a hand-net with 240-μm mesh. Sediment remaining in the core was stirred and the hand-net used to remove macroinvertebrates. Macroinvertebrate samples were preserved in the field with 5% formalin. Macroinvertebrates were sorted and transferred to 80% alcohol in the laboratory.

Many of the macroinvertebrate samples required subsampling due to excessive numbers of small organisms. These samples were passed through 1000- and 250-μm sieves. All material retained by the 1000-μm sieve was completely sorted. Subsamples (1/2, 1/4, and 1/8) were taken of the material retained by the 250-μm sieve. The size of the subsample was determined from an initial scan of one sample from each site per month. To assure that subsamples were representative, 10 samples were completely sorted using the above technique and each subsample enumerated separately. A chi-square contingency analysis (Zar 1984) indicated no significant ($p = 0.05$)

differences between subsamples for the total number of macroinvertebrates and common taxa. Most subsamples provided good estimates (within ± 15%) of the actual number of macroinvertebrates present in whole samples.

Macroinvertebrate functional feeding groups were determined following Merritt and Cummins (1984). Chironomids and *Hydra* were excluded from this analysis. Chironomids were not used because taxonomic resolution was not sufficient for detailed functional group analysis. *Hydra* was not used because of its unclear functional feeding designation in lotic systems. *Hydra* constituted <5% of the total number of macroinvertebrates at each site.

To facilitate some analyses, monthly periphyton and macroinvertebrate data were condensed to bimonthly, seasonal, or annual means. For example, macroinvertebrate data from December, January, and February were averaged to produce a single winter value.

Statistical Analyses

Simple bivariate relationships along the regulated river gradient were examined using Spearman rank correlations (Zar 1984). Whittaker's (1975) percentage similarity was used to determine faunal overlap between sites. Further multispecies analyses between sites were conducted with ordination techniques. Ordination is a mathematical treatment which allows samples to be organized on a graph so that those that are most similar, in both species composition and relative abundance, will appear closest together. It reduces a large, multidimensional data set into a low-dimensional (usually two or three) space. For both the percentage similarity and ordination analyses, the 28 predominant macroinvertebrate taxa were used (annual mean density ≥2 per sample, for at least one site). Most taxa were identified to species. Chironomidae, Oligochaeta, Ostracoda, and Simuliidae were not identified further. They were included in the analyses, each as a single taxon, although more complex relationships may have occurred at higher taxonomic resolution. All analyses were run with and without these groups and any major differences were noted.

Two ordination methods that have been used extensively in ecological studies are correspondence analysis (CA) and detrended correspondence analysis (DCA). DCA is a supposed improvement of CA (Hill and Gauch 1980), although there is controversy over the methods for correcting the assumed faults in CA (Wartenberg et al. 1987; Peet et al. 1988). One criticism of DCA is that the computer package DECORANA (Hill 1979) does not accomplish detrending in a mathematically elegant fashion (Wartenberg et al. 1987). Ter Braak (1988) provided an alternative (detrending-by-polynomials) in the computer package CANOCO. Both CA and the different methods for determining DCA were applied to the data set. Logarithmic transformations were used to reduce the effect of extreme abundance values (Gauch 1982).

The CA and DCA axes can be interpreted in terms of measured environmental variables using correlation analysis. This is a common technique used in ecological studies (e.g. Whittaker 1987; Matthews and Robison 1988). Recently, Ter Braak (1986, 1988) has combined this two-step approach into a single analysis, canonical correspondence analysis (CCA), an extension of CA. It can also be detrended (DCCA).

CCA and DCCA are constrained ordination techniques that analyze relationships between species abundances and environmental factors simultaneously. Ordination axes are linear combinations of environmental variables (Ter Braak 1986; Ter Braak and Prentice 1988). The environmental variables can be represented by arrows on an ordination diagram with length proportional to their influence. Moreover, their proximity to an axis indicates a possible environmental interpretation of that axis.

Results

Physical–Chemical Gradient

Physical and chemical factors exhibited various longitudinal patterns in the regulated Colorado River. Most chemical variables showed relatively little change over the first five sites below the impoundment, with any noticeable changes occurring from sites C5 to C6 (total hardness, total dissolved solids, and bound CO_2; Table 1). The river was well oxygenated along the entire study section. The pH was circumneutral at the two near-dam sites and exhibited a wider range from site C3 (1.4 km below the impoundment) downstream. Diel fluctuations in pH during the latter part of summer and early autumn, absent from the two near-dam sites, were partially responsible for this pattern. All chemical variables were within normal levels for similar high-elevation Rocky Mountain streams (Pennak 1977; Ward 1986). The substratum at each site consisted predominantly of cobble and pebble (Table 1). At each site, cobble > pebble > gravel (except site C6, where pebble ≈ gravel); these three size fractions collectively constituted over 90% of the mineral substratum. The proportion of sand generally increased downstream, with distinct increases between sites C1 and C3. Maximum value of sand occurred at site C6 (9.6%).

Temperature data (Fig. 2) showed a distinct downstream gradient with winter-warm and summer-cool temperatures near the dam. Ice was present at sites C4–C6, but only site C6 had complete ice cover for a prolonged period during this study.

Flow characteristics are generally predictable and constant below Granby Reservoir (30-yr record, Rader and Ward 1989a). Discharge from the reservoir to the river are minimal allowable flows that change according to legally established time schedules. Average discharge is 1.3 m^3/s (32 yr, U.S. Geological Survey records). Typically, the flow remains at approximately 0.6 m^3/s from September through April, increases to about 2.3 m^3/s from May through July, and then drops to approximately 1.1 m^3/s during August. This pattern was consistent for sites C1–C5 during this study, except for 9–16 June when flows ranged from 3.4 to 7.8 m^3/s. It was unlikely that this increased discharge disturbed the system (see Rader and Ward 1988).

Site C6 had higher flows during some months due to the influence of regulated Willow Creek (Fig. 2). Willow creek discharge was 1.1 m^3/s during November–February and then decreased to ≤0.2 m^3/s from March to mid-May. Flow then ranged from 3.4 to 11.3 m^3/s until mid-June, when it decreased again to ≤0.2 m^3/s for the remainder of the study period. However, from the latter part of June through October, Willow Creek was dry most of the time. The riffle at site C6 was also at least 50% wider than at upstream sites, thus reducing some effects of increased discharge. Willow Creek did not appear to affect the temperature regime at site C6 (Fig. 2).

Average velocities were similar between sites (usually ± 10 cm/s) and no downstream pattern was detected. Average velocities across all sites during the different flow regimes (i.e.

TABLE 1. Annual ranges of sampling site widths and chemical variables and average percentage of total substratum by weight for each size category ($n = 4$).

	Sampling site					
	C1	C2	C3	C4	C5	C6
Width (m)	11.0–12.5	8.5–10.0	12.5–14.5	14.5–15.5	14.5–15.5	19.0–22.0
O_2 (% saturation)	>100	>100	>100	>100	>100	>100
pH	6.9–7.3	6.9–7.3	7.0–8.3	7.2–8.3	7.2–8.2	7.5–8.3
Total hardness (mg/L)	18–24	18–24	18–26	22–30	22–38	28–60
Total dissolved solids (mg/L)	21–30	21–36	20–31	26–39	30–44	50–73
Bound CO_2 (mg/L)	7.0–10.0	7.0–10.5	7.5–11.5	8.0–11.5	10.0–20.0	12.5–24.0
Nitrate-nitrogen (mg/L)	<0.05–0.09	<0.05–0.07	≤0.05	<0.05	<0.05	≤0.05
Substratum size (average %)						
Cobble (52–247 mm)	60.7	63.0	54.2	54.9	58.7	53.0
Pebble (12–52 mm)	25.6	20.6	22.6	20.1	19.9	18.6
Gravel (2–12 mm)	13.3	12.9	15.5	17.7	15.7	18.7
Sand (75 μm – 2.0 mm)	0.3	3.4	7.6	7.2	5.6	9.6
Silt–clay (<75 μm)	<0.1	<0.1	<0.1	<0.1	<0.1	0.1

0.6, 2.3, and 1.1 m^3/s) were 23–25, 35–55, and 25–42 cm/s, respectively.

Food Resource Gradient

Periphyton standing crop exhibited a unimodal pattern, with maximum biomass occurring at site C2 (Fig. 3). Filamentous chlorophytes and bryophytes predominated at sites C1–C3 whereas diatoms were prevalent at sites C4 and C5. A subsequent increase in filamentous algae and a dense organic matrix characterized the periphyton at site C6. Organic seston remained at similar concentrations over all sites during winter and autumn (Fig. 3). In spring and summer, a distinct increase occurred at site C6.

Spearman rank correlations between the standing crop of 75–250 μm FPOM (Fig. 4, top) and distance downstream from the dam were significant during winter, spring, and summer ($r_S = 1.0$, $p < 0.01$, for each season). The trend was similar for autumn ($r_S = 0.83$, $p = 0.10$). Mass of the 250–1000 μm FPOM fraction (Fig. 4, bottom) increased significantly with distance from the impoundment during all seasons ($r_S = 1.0$, $p < 0.01$, winter, spring, and autumn; $r_S = 0.89$, $p = 0.05$, summer). Increased flow from Willow Creek in May and June could have lead to higher amounts of FPOM at site C6 during the summer, although FPOM levels were usually highest at this site during the study period.

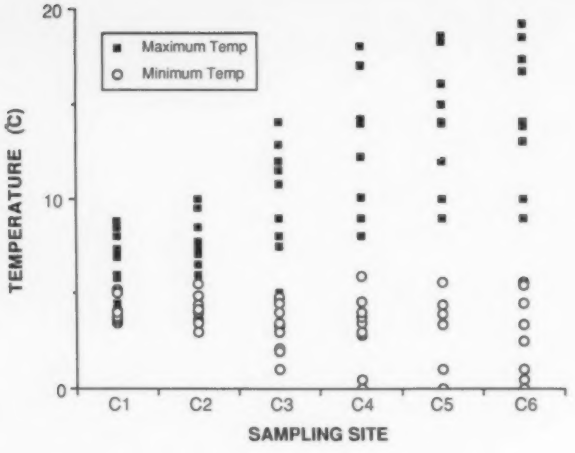
The mass of deciduous leaves (Fig. 5) increased significantly with distance from the dam during all seasons ($r_S = 0.94$, $p = 0.02$, winter and summer; $r_S = 1.0$, $p < 0.01$, spring and autumn). AFDM of conifer needles did not increase significantly downstream of the impoundment during any season (Fig. 5), although high values were observed during summer (site C3) and autumn (sites C4 and C5). The wood fraction exhibited a significant downstream increase during spring and summer ($r_S = 1.0$, $p < 0.01$ and $r_S = 0.89$, $p = 0.05$, respectively, Fig. 5), with similar trends during winter and autumn ($r_S = 0.83$, $p = 0.10$ and $r_S = 0.77$, $p = 0.13$, respectively). Large woody material (e.g. logs, fallen trees) was mostly absent from all sites. Standing crop of the "other" CPOM fraction (e.g. grass, roots, buds) increased significantly with distance from the dam only during winter ($r_S = 0.94$, $p = 0.02$, Fig. 5), with a similar pattern indicated during summer and autumn ($r_S = 0.77$, $p = 0.13$, for both seasons). As for FPOM, the higher summer values of "other" CPOM at site C6 may have been caused by increased flows from Willow Creek, but this trend was not observed for leaves, needles, or wood.

Macroinvertebrate Responses

Total macroinvertebrate abundances were high at sites C1–C3. Abundance values declined precipitously between sites C3 and C4 and remained at levels similar to site C4 at the two farthest downstream sites (Fig. 6). Taxonomic richness increased with distance from the dam; sites C5 and C6 had comparable high values (Fig. 6). Insects comprised >90% of the total zoobenthos at all sites. Chironomids, simuliids, and baetid mayflies (>75% of the total Ephemeroptera) predominated at sites C1–C3.

Plecoptera and Trichoptera increased in abundance downstream, while Diptera declined (Fig. 7). Ephemeroptera exhibited a unimodal distribution, with peak abundances occurring at site C3 and lowest values at site C6 (Fig. 7). Coleoptera were represented by two species, *Heterlimnius corpulentus*, with peak densities at site C4, and *Optioservus* sp., which had highest abundance values at site C6. Coleoptera were only collected occasionally from sites C1–C3. The density of noninsect macroinvertebrates (e.g. Acarina, *Hydra* spp., Oligochaeta, *Polycelis coronata* (Turbellaria), and Ostracoda) decreased downstream from the impoundment.

Amphinemura banksi was the only plecopteran to exhibit peak (although low overall) densities near the dam whereas chloroperlids (predominantly *Triznaka signata*) comprised most of the stoneflies at farther downstream sites. Approximately 20 species of Trichoptera were found, with 10 predominant spe-



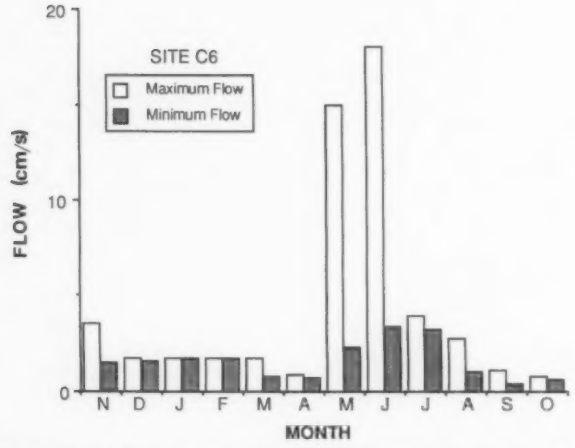
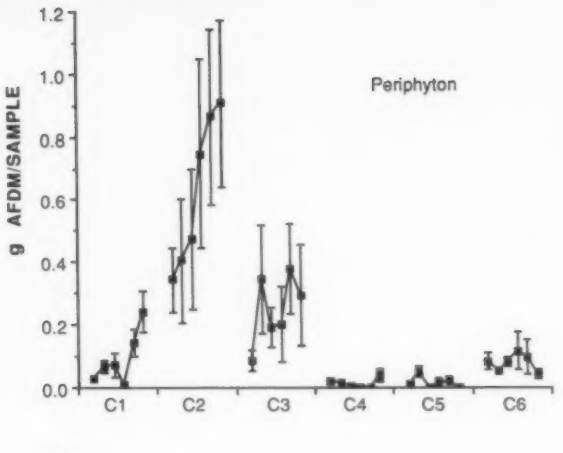


FIG. 2. Monthly flow (at site C6) and temperature data for the study period. Discharge data for site C6 were obtained from gauging stations located near sites C2 and C5 and directly below Willow Creek Reservoir.



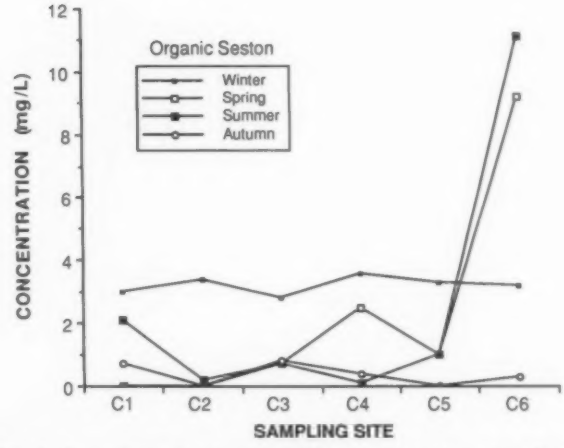


FIG. 3. Downstream trends of periphyton and organic seston. Periphyton is represented as bimonthly means ± 1 SE ($n = 6$; $n = 3$, June at site C6). The six squares at each site represent values for November–December, January–February, March–April, May–June (June only, site C6), July–August, and September–October, respectively. Seasonal values from one sample per site are shown for organic seston.

cies. *Brachycentrus americanus, Glossosoma spp., Lepidostoma ormeum*, and *Rhyacophila coloradensis* exhibited highest abundances in the middle reaches. *Rhyacophila coloradensis* was the predominant caddisfly at near-dam sites. Maximum abundances of *Brachycentrus occidentalis, Cheumatopsyche* sp., *Hydropsyche* spp., *Protoptila coloma*, and *Psychomyia flavida* occurred at site C6; these taxa were rarely or never found at upstream sites (except *Hydropsyche* spp.). Baetid mayflies had high abundance levels at sites near the dam, with peak densities occurring at site C3. Especially high numbers of baetids were observed at site C3 during May, September, and October. Concomitant with the downstream decline of *Baetis* spp. was a rise in *Epeorus* spp. (*E. albertae* and *E. longimanus*), *Ephemerella infrequens*, and *Paraleptophlebia heteronea* abundances at sites C4 and C5. They subsequently declined at site C6, which had the lowest overall number of Ephemeroptera.

The longitudinal distribution of macroinvertebrate functional feeding groups (sensu Merritt and Cummins 1984) in the Colorado River may provide insight into the influence of downstream changes in food resources (Fig. 8). The proportion of collector–filterers, organisms that feed on organic material suspended in the water column, was highest at near-dam sites and at site C6. Shredders, species that feed on coarse sedimentary detritus, generally increased with distance from the impoundment. Collector–gatherers, organisms that feed on fine sedimentary detritus, exhibited peak values at sites C3 and C4. This was the predominant functional group at all sites, except C1. Scrapers, species that feed on periphyton, remained at comparable levels from sites C1 to C3, dropped slightly in relative abundance at site C4, and remained at levels similar to site C4 at the farthest downstream sites. The contribution made by predators increased gradually downstream, but they usually comprised the smallest portion of the functional groups.

A specific example of a functional feeding group longitudinal pattern was examined using the filter-feeders. Total filter-feeder abundance (*Arctopsyche grandis, B. americanus, B. occidentalis, Cheumatopsyche* sp., *Hydropsyche* spp., and Simuliidae) was highest at site C1, decreased to site C3, and then increased through site C6 (Fig. 9, top). However, the amount of organic seston was generally highest at site C6

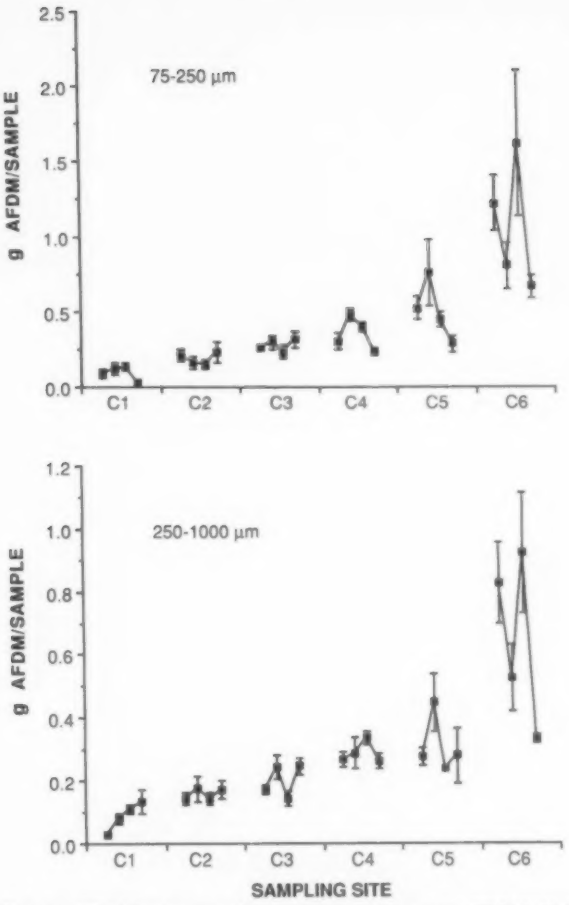


FIG. 4. AFDM for the two size fractions of sedimentary FPOM. Values are shown as seasonal means ± 1 SE (n = 3). The four squares at each site represent values for winter, spring, summer, and autumn, respectively.

(Fig. 3). Examining the individual taxa, with hydropsychid caddisflies combined, presents a more detailed pattern (Fig. 9, middle and bottom). Simuliidae were predominant at sites near the dam, *B. americanus* was numerically dominant in the middle reaches, and *B. occidentalis* and the hydropsychid caddisflies reached peak densities at the farthest downstream site (C6).

Multispecies Responses along the Complex Gradient

Results from Whittaker's (1975) index of percentage similarity (P_S) are shown in Fig. 10. In general, P_S values declined with increasing distance between two sites and adjacent sites exhibited highest overall P_S. However, P_S values between sites C3 and C4 and between sites C5 and C6 were relatively low, indicating areas of greater change in faunal composition. The pattern was similar when chironomids, oligochaetes, ostracods, and simuliids were excluded from the analysis; their removal merely accentuated the differences between near-dam and farther downstream sites. For example, P_S between sites C1 and C6 changed from 56.8% (with the four taxa included) to 14.5% (without).

Because a strong distortion ("arch effect") resulted in the CA, making interpretation difficult and perhaps misleading, only the DCA results will be discussed. Both DCA analyses (DECORANA, Hill 1979; CANOCO, Ter Braak 1988) produced similar patterns, but two differences did occur. The first was a reversal in sample (site) score arrangement. This did not change interpretations. The second difference was some alteration in sample score distribution along the second DCA axis. CANOCO scores for site C2 samples showed increased dispersion, while scores for sites C3, C4, and C5 were compressed along the second axis when compared with the DECORANA results. Because the second DCA axis had a relatively low eigenvalue (lower variance explained), interpretation of this axis may be superfluous. Either method appears to be useful for recovering the Colorado River gradient patterns. Only the DCA results produced by CANOCO are shown (Fig. 11). Points (symbols) that are in close proximity have similar species composition and abundances. Results were similar when Chironomidae, Oligochaeta, Ostracoda, and Simuliidae were excluded. Only the results for the full data set will be emphasized herein. Downweighting of rare species did not produce noticeable differences.

Clearly, the dominant pattern was the distinct downstream change in faunal composition along the first DCA axis (Fig. 11). Maximum change occurred over the first 3 km below the impoundment (sites C1–C4). There was a substantial shift in macroinvertebrate assemblages between sites C1 and C2, a distance of only 0.25 km. There was also rapid faunal change exhibited between sites C2 and C3 (approximately 1.0 km apart) and between sites C3 and C4 (1.3 km apart). Sites C4 and C5 (2.1-km separation) had similar faunal communities. Another shift in community composition occurred between sites C5 and C6, although the change resulted over a distance of approximately 7.0 km.

CCA and DCCA were applied to the mean seasonal abundance values of the 28 predominant macroinvertebrate taxa. This allowed comparisons with those food resource variables that were only collected seasonally. Environmental and food resource parameters included in the analyses were maximum and minimum temperatures, periphyton (seasonal mean biomass), organic seston, two FPOM fractions (75–250 and 250–1000 µm), and the four CPOM categories (deciduous leaves, conifer needles, wood, and other material). The results from CCA exhibited a distinct arch effect (as for CA) and were not considered further.

Sample scores from the DCCA (Fig. 12) revealed a clear downstream change in taxa composition, as was shown in DCA. Sites near the dam were influenced by higher minimum temperatures (winter-warm) and greater periphyton mass (indicated by direction and magnitude of arrows, Fig. 12). The slight increase in periphyton standing crop at site C6 was not indicated in the analysis (see Fig. 3). Data on conifer needles contributed little to the analysis (vector coordinates near the origin) and were removed from Fig. 12.

Higher maximum temperature and an increase in most food resource variables were observed with progressively greater distance from the impoundment (Fig. 12). The longer vectors for deciduous leaves and the two FPOM size fractions indicated the importance of these three variables along the regulated river gradient. Minimum temperature, periphyton mass, and organic seston concentration showed proximity to DCCA axis 2, indicating their influence on that axis. Between sites C2 and C4 was an area of rapid change in temperature and periphyton standing crop. This may have been responsible for the dispersion of sample scores, that are a reflection of faunal changes,

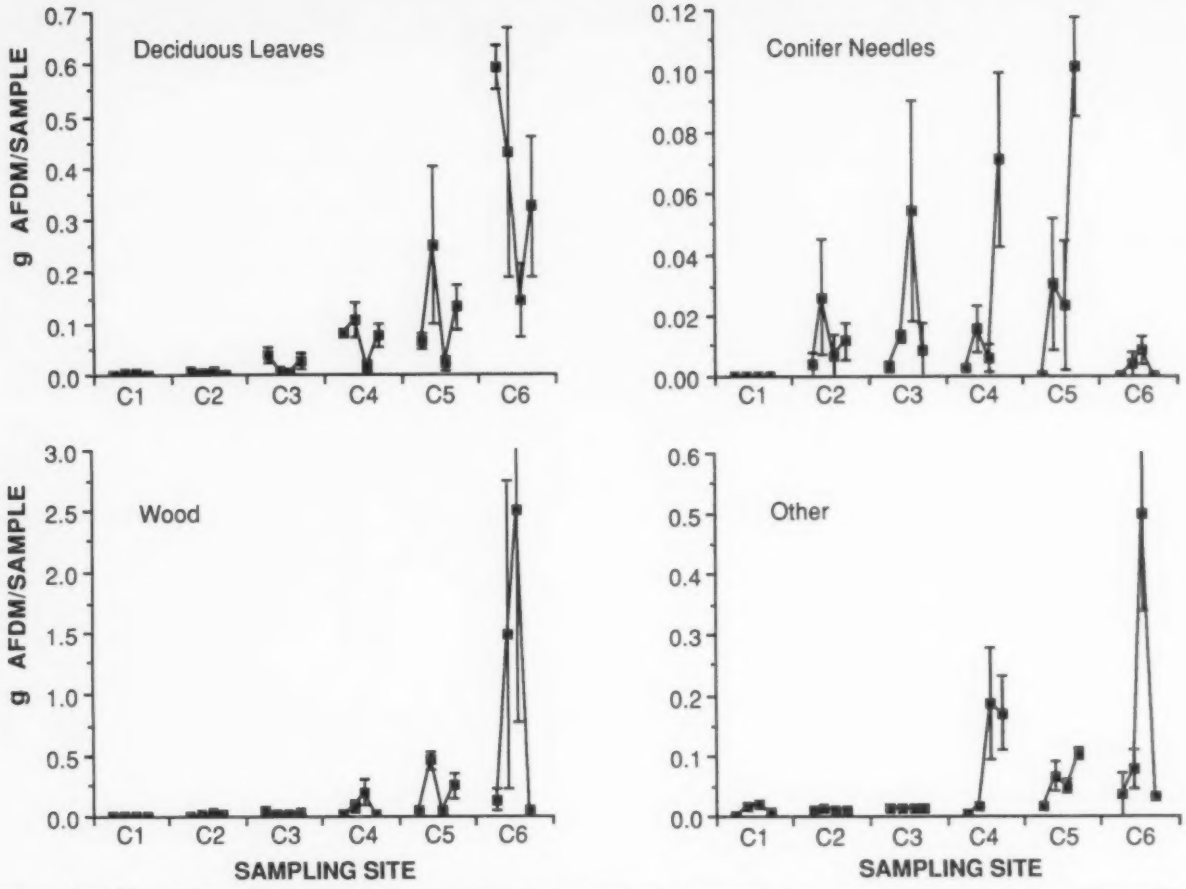


FIG. 5. AFDM for the four categories of sedimentary CPOM. Values are shown as seasonal means ± 1 SE (n = 3). The four squares at each site represent values for winter, spring, summer, and autumn, respectively.

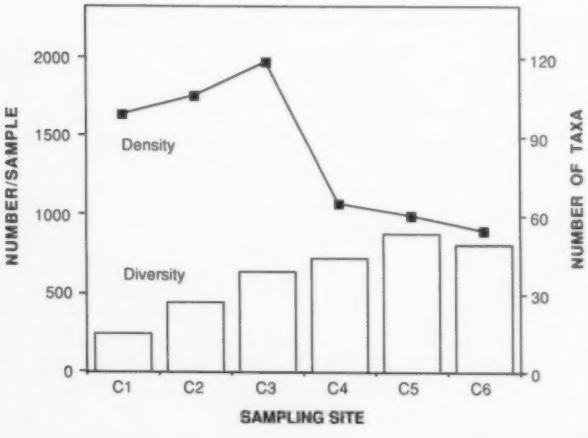


FIG. 6. Annual average number of zoobenthos per sample (line) and total number of taxa (bars) at each sampling site. Number of taxa (mostly species) excludes rare species (i.e. those that occurred in <2 mo). Chironomids were not identified further than family.

for sites C2 and C3 along DCA axis 2 (Fig. 11). However, the low axis 2 eigenvalues for both DCA and DCCA make any distinct interpretation difficult.

Discussion

Overall macroinvertebrate responses to the regulated gradient indicated three areas of rapid community change. Sites C1–C3 consisted predominantly of chironomids, simuliids, and *Baetis* spp. (>80% of the total macroinvertebrates). This is similar to the macroinvertebrate composition found in the headwaters of the Colorado River (Ward et al. 1986). However, diversity nearly doubled between sites C1 and C2 and greatly increased again between sites C2 and C3 (Fig. 6). This, combined with changes in the relative abundances of chironomids, simuliids, and *Baetis* spp., accounted for the distinct community changes within the first 1.4 km below the impoundment (DCA and DCCA, Figs. 11 and 12). Sites C4 and C5 were areas that had more equitable zoobenthic communities with few dominant species. These communities changed gradually downstream to site C6 (Figs. 11 and 12).

Temperature can play a major role in the distribution, development, and growth of aquatic macroinvertebrates (Vannote and Sweeney 1980; Ward and Stanford 1982). Temperature

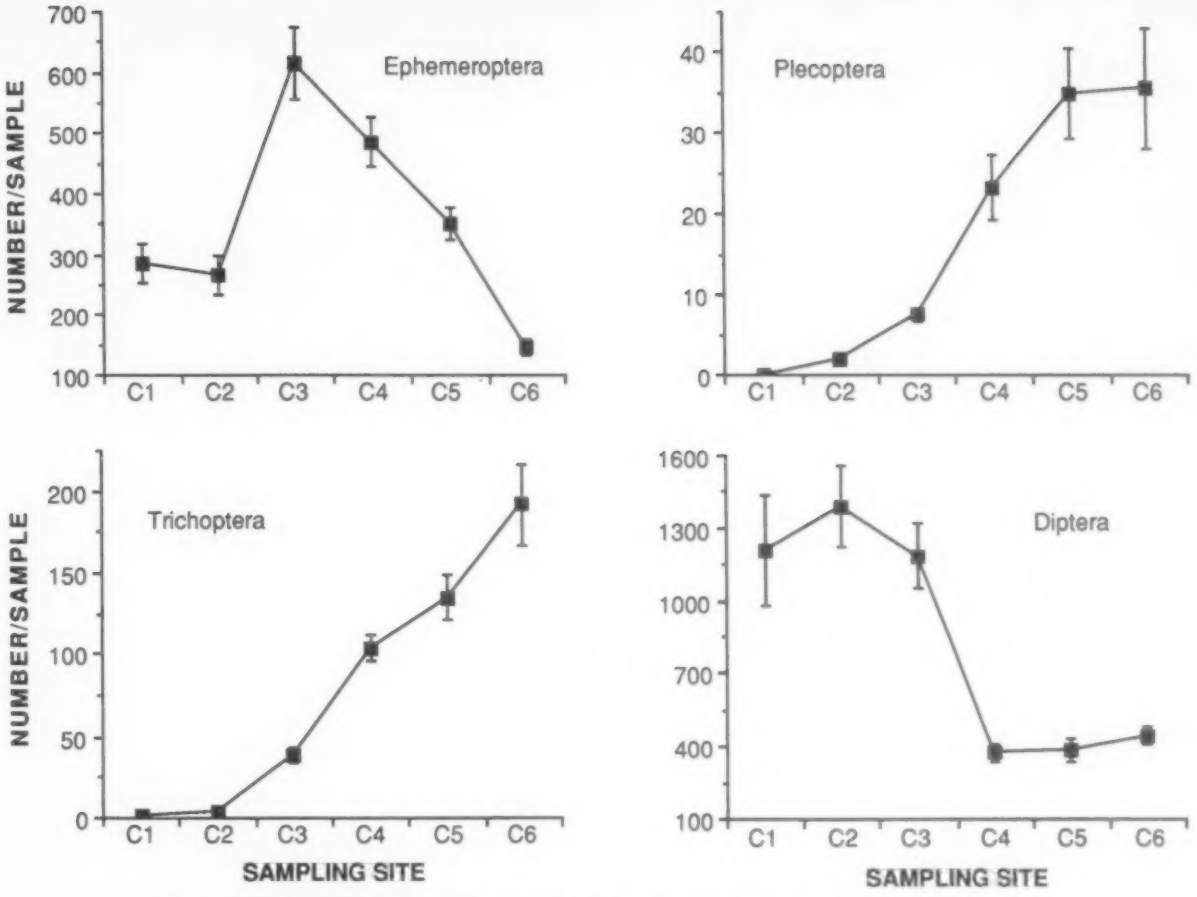


FIG. 7. Annual mean number (± 1 SE) per sample of the major insect orders (n = 48; n = 44, at site C6).

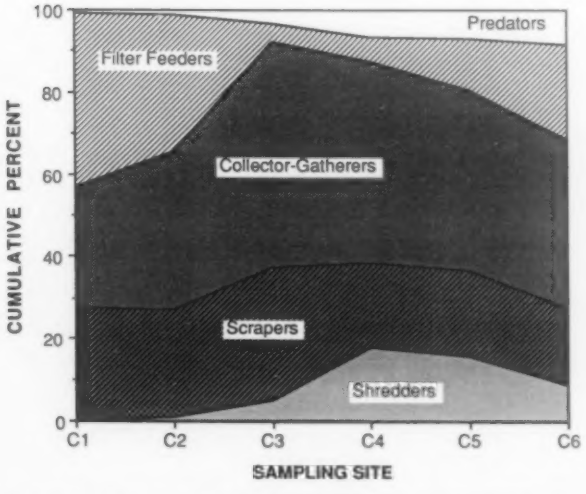


FIG. 8. Relative contributions (by abundance) of macroinvertebrate functional feeding groups (sensu Merritt and Cummins 1984) along the regulated Colorado River longitudinal gradient.

variation exhibited a strong downstream gradient in the Colorado River. This is a common occurrence in streams below hypolimnial-release dams (Ward 1982, 1985). Ward (1984) speculated that the partially braided stream channel below Granby Reservoir provided thermal refugia for some macroinvertebrate taxa that otherwise could not complete their life history in the thalweg. These sites of greater temperature range may partially account for the rapid increase in the number of taxa between sites C1 and C3. However, the thermal character of these small areas did not contribute appreciably to the overall temperature recovery pattern displayed in the Colorado River.

The large standing crop of periphyton (Fig. 3) at sites near the Granby Reservoir dam may be attributable to both abiotic (e.g. water clarity, substrate stability, absence of ice action, see Lowe 1979) and biotic factors (e.g. lack of grazers, Spence and Hynes 1971; Lamberti and Resh 1983). The amount and type of periphyton present can have profound effects on the ability of many macroinvertebrates to inhabit an area (Ward 1976; Dudley et al. 1986). Dense algal and bryophyte growth changes the structural habitat by limiting attachment sites, precluding mobility and reducing local microcurrent velocity. However, this reduction of local velocities may favor some zoobenthos. As periphyton mass decreased and became patchy downstream, additional fauna could exit. The peak densities of

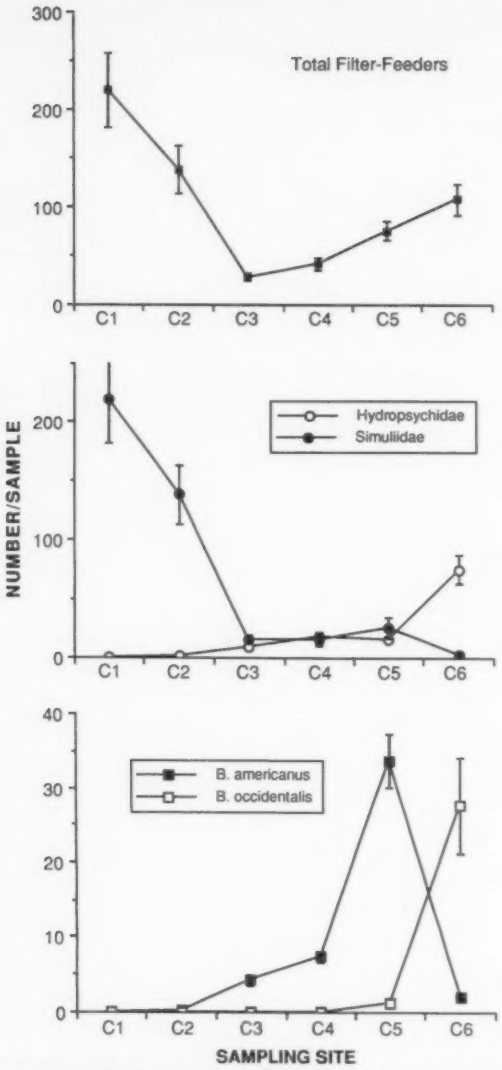


FIG. 9. Top graph shows annual mean number (± 1 SE) per sample of total filter-feeders. Middle and bottom graphs depict the annual mean number (± 1 SE) of organisms per sample for the filter-feeders *A. grandis*, *Cheumatopsyche* sp., and *Hydropsyche* spp. (combined hydropsychid caddisflies), Simuliidae (black flies), and *B. americanus* and *B. occidentalis* (brachycentrid caddisflies) (n = 48; n = 44 at site C6, for all graphs).

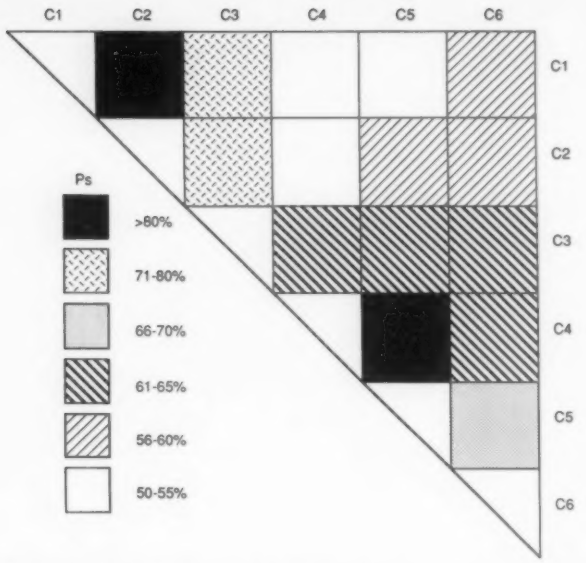


FIG. 10. Matrix of percentage similarity (P_s) between sampling sites based on annual means of the predominant taxa.

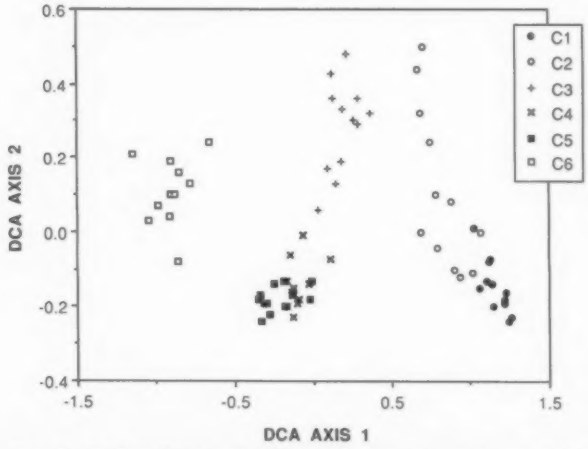


FIG. 11. DCA ordination diagram for the macroinvertebrates of the Colorado River (CANOCO, Ter Braak 1988). Symbols represent monthly DCA sample scores for each site. Eigenvalues for the first three DCA axes are 0.277, 0.040, and 0.027, respectively.

the mineral scrapers *Glossosoma* spp. and *Epeorus* spp. in the middle reaches may be a response to the lower mass, diatom-based periphyton. Moreover, the primary energy source for the river appeared to be predominantly autochthonous near the dam and perhaps for some distance downstream. Site C6 (12.0 km below the dam) also had high periphyton biomass, although usually less than sites near the dam, that consisted primarily of decaying organic matter, diatoms, and filamentous algae. In addition, some organisms (chironomids, *Psychomyia flavida*, hydropsychids) built retreats or tubes on the top surfaces of stones at site C6, perhaps both using the organic matrix in construction and contributing to it by trapping organic matter. The organic matrix at site C6 was an important food resource because it was qualitatively different from periphyton at sites near the dam and did not appear to limit habitat use by some organisms.

The amount of allochthonous food resources present in a river can greatly influence macroinvertebrate distributions (Culp et al. 1983). The increase in small particle detritivores (e.g. *P. heteronea*, see Rader and Ward 1989b) and shredders (e.g. *L. ormeum*) along the regulated river gradient may be a response to increased levels of allochthonous material with distance from the dam (Figs. 4, 5, and 12). Although shredders are generally absent directly below the impoundment, microbial processing of leaf detritus can still occur (Short and Ward 1980). *Lepidostoma* spp. feed upon conifer needles in Oregon

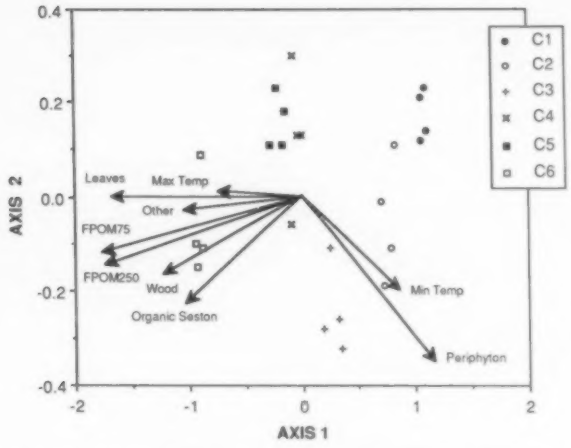


FIG. 12. DCCA ordination diagram. Symbols represent seasonal sample scores for the macroinvertebrates at each site. Environmental variables are represented by arrows. FPOM75 and FPOM250 represent the 75–250 and 250–1000 μm FPOM fractions, respectively. Eigenvalues for the first three DCCA axes are 0.252, 0.015, and 0.014, respectively.

streams (Sedell et al. 1975). The possible processing of this refractory material by *L. ormeum* may be important for the overall energy input to the Colorado River. However, no statistically significant relationships were found between the mass of conifer needles and the abundance of *L. ormeum*. Although the level of sedimentary detritus (FPOM and CPOM) usually increased significantly with distance from the dam, the numbers of macroinvertebrates that feed on this resource generally declined at the farthest downstream site (C6), where detritus levels often reached maximum levels. This indicated that other factors (e.g. temperature, periphyton standing crop) may be more important in limiting detritivore distributions directly below Granby Reservoir.

The combined abundance of filter-feeders exhibited a bimodal pattern that when examined more closely yielded distinct species responses along the gradient (Fig. 9). The concentration of organic seston was usually similar at all sites, except during spring and summer when maximum values were recorded at site C6 (Fig. 3). The high density of simuliids at sites near the dam was anomalous, as their populations are often suppressed below deep-release impoundments (Bass and Armitage 1987; but see Voelz and Ward 1989). Simuliids require "clean" surfaces for attachment (Colbo and Wotton 1981), indicating that they found open patches near the dam or they somehow attached to filamentous algae and bryophytes. Inputs of plankton and bacteria from the reservoir, although low in biomass, must be sufficient to maintain the simuliid populations. As the type and quality of seston changed downstream (N.J. Voelz and J. V. Ward, unpubl. data), each species responded uniquely as shown by the distinct distributional patterns of filter-feeders. In addition, there is evidence that simuliids are competitively inferior relative to other filter-feeding insects (Hemphill 1988; Hershey and Hiltner 1988). This could also restrict their distribution primarily to sites near the dam. The filter-feeding caddisflies *B. americanus* and *B. occidentalis* usually coexist in a stream (Winget 1984; Hauer and Stanford 1986), although some spatial separation has been noted (Gallepp 1977). This was not true in the Colorado River. The disjunct distributions of the ecologically similar *B. americanus* and *B. occidentalis* suggest the possibility of biotic interactions. Gallepp (1974) observed interspecific and intraspecific interactions between *Brachycentrus* larvae. In addition, these species might have responded to changes in organic seston quantity or quality that occurred between sites C5 and C6.

The River Continuum Concept (RCC, Vannote et al. 1980) predicts downstream shifts in the relative abundance of functional feeding groups as food resources change along the longitudinal profile of river systems. In general, shredders are primarily found in the headwaters; collectors (both filter-feeders and gathers) are important in all reaches, but are virtually the only nonpredaceous invertebrates in lower reaches; grazers reach maximum densities in the middle reaches; and predators maintain similar low relative abundances along the entire stream. This initial formulation was derived from studies of deciduous forest streams in eastern North America. The applicability of the RCC to other geographic areas has been questioned (Winterbourn et al. 1981; Ward 1986), but modifications of the RCC have produced a "sliding scale" to emphasize that different types of streams (e.g. desert, forest) enter the continuum at different points (Minshall et al. 1985).

Because Granby Reservoir disrupts the resource and physical–chemical gradients that occur along the river continuum (Ward and Stanford 1983), is the 12-km regulated reach analogous to the headwater to middle reach segment of a free-flowing river? In other words, do conditions immediately below the dam mimic conditions expected in a headwater stream and then rapidly change downstream to resemble conditions expected in a sixth-order river? Only the increase of filter-feeders at the farthest downstream site followed the predictions of the RCC. However, the high relative abundance of filterers at sites C1 and C2 was counter to the expected trend. This is not surprising because the reservoir may supply relatively large amounts of high-quality organic seston that would not be available in a headwater stream section.

Comparisons between our study and research conducted in free-flowing rivers are useful for determining if the shorter regulated river gradient is similar to an extended segment of an unimpounded river. In addition, insight can be gained into the recovery potential of streams disrupted by impoundments. A study on the St. Vrain River, located on the eastern slope of the Colorado Rocky Mountains, provides sufficient detail and will be used for comparisons (Ward 1986). The St. Vrain River was sampled at 11 sites over an elevation of 1500–3400 m a.s.l. (55-km study reach). Only data for the first eight sampling sites, the latter areas at similar elevations to our study, will be emphasized. Substrata characteristics and levels of dissolved O_2 and nitrate were similar in both rivers. Bound CO_2, total dissolved solids, and temperature variation increased downstream in both studies. However, the temperature range observed at site C6 in the Colorado River corresponded more with the St. Vrain site located at 1700 m a.s.l. (35 km from the source). Moreover, winter temperature reached 0°C at all sites on the St. Vrain, but only at sites C4–C6 in the present study.

Organic seston concentrations were low over most sites in both rivers. The highest levels were recorded at the farthest downstream site in the St. Vrain River (1500 m a.s.l.) and at site C6. The longitudinal pattern of sedimentary detritus exhibited an opposite trend in the two rivers. Periphyton standing crop was highest at alpine sites (>3000 m a.s.l.) in the St. Vrain River and at sites near the dam in the Colorado River.

In addition, bryophytes and filamentous chlorophytes comprised the greatest proportion of periphyton at these sites.

The macroinvertebrate communities of both rivers were composed predominantly of insects (>90% by number). Total density and diversity increased downstream in the St. Vrain River whereas only diversity increased downstream in the Colorado River. The longitudinal diversity pattern was sigmoidal in both rivers, with the greatest increases occurring in the middle reaches. Of the major insect groups, only Trichoptera and Diptera exhibited a similar distribution pattern. Highest densities of Trichoptera in the St. Vrain were recorded at the montane/foothills ecotone (~2400–2600 m a.s.l.) and at site C6 in the Colorado River (2400 m a.s.l.). Interestingly, the highest number of hydropsychid caddisflies (*Cheumatopsyche* and *Hydropsyche*) occurred at 1500 m a.s.l. in the St. Vrain River whereas they were most abundant at site C6, approximately 1000 m higher in elevation. Both of these sites also had the highest concentrations of organic seston. Peak simuliid densities were found in the headwater (alpine) areas of the St. Vrain River and at sites directly below Granby Reservoir, where seston concentrations were low. In the functional feeding group analyses, only the collector–gatherers exhibited a similar longitudinal distribution pattern in both rivers, as they were abundant at all sites. In addition, there were relatively high abundances of scrapers in the headwater area of the St. Vrain River and at sites directly below the impoundment.

These comparisons illustrate that although the reach of the regulated Colorado River that we studied has many similarities with a free-flowing stream over broad elevational range, some major differences occurred. Stream regulation imposes several constraints on lotic biota that do not occur in free-flowing rivers. For example, although temperature variation is reduced in headwater areas of mountain streams, winter minimum temperatures reach 0°C. Winter temperatures at sites directly below Granby Reservoir rarely go below 3°C. In addition, sedimentary detritus at all sites in the St. Vrain River was primarily allochthonous whereas in the regulated Colorado River, sedimentary detritus at sites near the dam was primarily autochthonous. Thus, regulated streams are unique environments that only partially resemble free-flowing rivers. Nonetheless, by comparing free-flowing with regulated rivers, insight is gained into the common features of river ecosystems and how impoundments disrupt the natural functioning of these systems. Moreover, the recovery potential of streams below impoundments is indicated by the many similarities found between the farthest downstream site in the Colorado River study section and sites at a corresponding elevation or with similar environmental characteristics in the St. Vrain River.

There have been few studies on biotic and abiotic gradients in regulated high-elevation streams, over a spatial scale comparable with our study. Ward (1974) conducted a study similar to the present one, with four sampling sites located below a hypolimnial-release impoundment (8.5-km study reach) on the South Platte River, Colorado (~2000 m a.s.l.). Similarities between the regulated Colorado and South Platte rivers include downstream increases in temperature variation, suspended organic matter, and species richness. There were differences in the longitudinal patterns of periphyton biomass and density of macroinvertebrates.

Insects comprised 75% by number of the total macroinvertebrates in the South Platte River versus >90% in the Colorado River study section. Of the major insect orders, only Plecoptera exhibited a similar longitudinal spatial pattern. Plecoptera in Ward's study were represented by a single species, found in relatively low numbers. The distribution pattern of total filter-feeders was similar in both rivers. However, a major difference was that Simuliidae, although abundant directly below both dams, reached highest densities 8.5 km below the South Platte impoundment. A pattern opposite that found in the Colorado River.

An identical study was conducted in the Blue River, Colorado, during the same time as the present study (Voelz and Ward 1989, 1990). The Blue River (~2600 m a.s.l.) is also a western slope Rocky Mountain river, regulated by a deep-release storage impoundment. As for the Colorado River, there were minimal changes in chemical parameters with distance from the dam. Temperature variation and substrata characteristics were similar for both rivers. Food resources exhibited strikingly similar longitudinal patterns, with most increasing downstream from the reservoirs. Periphyton standing crop was highest at near-dam sites in both rivers.

Macroinvertebrate diversity increased downstream from both impoundments, with the greatest change occurring in the first 3 km. However, the doubling of diversity observed in the Colorado River within 500 m below the reservoir was not detected in the Blue River. Insects comprised >80% of the total macroinvertebrates by number in both rivers, except at near-dam sites in the Blue River during summer, when large numbers of *Hydra* were found. Of the major insect orders, Ephemeroptera and Diptera exhibted similar longitudinal distribution patterns in both rivers. Primarily *Baetis* spp. accounted for the Ephemeroptera peaks observed at sites 1.4 km (Colorado River) and 2.3 km (Blue River) below the impoundments. Simuliids and chironomids were usually predominant directly below both reservoirs.

The abundance of filter-feeders was highest at near-dam sites in both rivers, and declined precipitously at farther downstream sites. In the Colorado River, a small increase in filterers was observed at the farthest downstream site. The abundance of hydropsychid caddisflies increased with distance from the dam in the Colorado River whereas *A. grandis* (the predominant hydropshychid in the Blue River) reached peak densities 2.3 km below the Blue River impoundment. *Brachycentrus occidentalis* was a predominant filter-feeder at the farthest downstream site in both rivers.

Application of DCA and DCCA to the macroinvertebrate and environmental data sets for each river revealed very similar patterns. A sequential faunal gradient was exhibited in both rivers, with the most rapid changes in the macroinvertebrate communities occurring within the first 2–3 km below each impoundment. This was primarily a consequence of species additions, not species replacements. The DCCA results identified downstream decreases in periphyton standing crop and minimum temperatures and downstream increases in most food resources and maximum temperatures as major variables structuring faunal assemblages in both rivers. These comparisons between the Blue and Colorado rivers illustrate that regulated high-elevation streams have many similarities and that predictable longitudinal biotic and abiotic patterns exist. Viewing regulated streams as disrupted continua makes comparisons more meaningful, as it provides an indication of the recovery potential of streams to perturbations. Moreover, the use of ordination techniques, such as DCA and DCCA, provides a standard with which complex data sets can be compared.

The interactions of a suite of complex environmental factors were important in determining the macroinvertebrate distribu-

tions observed in the Colorado River. A narrow thermal regime and high periphyton mass at sites near the dam could have eliminated those species dependent on thermal heterogeneity to complete their life cycle, those unable to use a primarily autochthonous resource base, or those that are physically precluded from using areas of dense periphyton growth. As the temperature recovered with distance from the dam, additional species were added. Moreover, food resources (FPOM, CPOM, organic seston) increased downstream and changed from an autochthonous to allochthonous base. Thus, it is futile to attempt to identify any one environmental factor as the primary determinant affecting macroinvertebrate distribution patterns.

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Temperature-Dependent Maximum Daily Consumption of Juvenile Salmonids by Northern Squawfish (*Ptychocheilus oregonensis*) from the Columbia River

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Vigg, S., and C. C. Burley. 1991. Temperature-dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. Can. J. Fish. Aquat. Sci. 48: 2491–2498.

Maximum daily consumption rate (C_{max} as ration or number) of northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River increased exponentially as a function of temperature. Predator weight did not explain a significant independent proportion of variation in C_{max}. The mean maximum daily ration, determined from replicate ad libitum feeding on juvenile Pacific salmon (*Oncorhynchus* spp.), was 0.47, 0.70, 3.39, and 4.50 $cg \cdot g^{-1}$ at 8.0, 12.5, 17.0, and 21.5°C, respectively. The corresponding mean daily number eaten was 0.50, 1.17, 4.25, and 7.01 prey per predator at the four increasing temperatures. To quantify the temperature-dependent consumption relation, replicate C_{max} data within the preferred temperature range were fitted to exponential and exponential sigmoid models. On the basis of a knowledge of thermal relations of northern squawfish, we combined hypothetical C_{max} data at temperature extremes with our mean experimental results to fit an algorithm suitable for use in simulation modeling. Both the generalized gamma and biological-rate (Thornton and Lessem. 1978. Trans. Am. Fish. Soc. 107: 284–287) algorithms were suitable to describe a hypothetical temperature–C_{max} model over the entire environmental temperature range of 0–27°C observed in the Columbia River.

Le taux de consommation quotidien maximal (C_{max} en termes de ration ou de nombre) de cyprinoïdes d'Orégon (*Ptychocheilus oregonensis*) du fleuve Columbia a augmenté exponentiellement en fonction de la température. Le poids des prédateurs n'a pas expliqué une proportion indépendante importante de variation de C_{max}. La ration quotidienne maximale moyenne, déterminée à partir d'une consommation à volonté répétée de jeune saumon du Pacifique (*Oncorhynchus*), a été de 0,47, 0,70, 3,39 et 4,50 $cg \cdot g^{-1}$ à 8,0, 12,5, 17,0 et 21,5°C respectivement. Le nombre quotidien moyen correspondant consommé a été de 0,50, 1,17, 4,25 et 7,01 proies par prédateur à ces mêmes températures croissantes. Pour quantifier la relation de la consommation en fonction de la température, des valeurs répétées de C_{max} dans la gamme optimale de température ont été appliquées à des modèles exponentiel et sigmoïde exponentiel. Connaissant les relations thermiques régissant le cyprinoïde du nord, nous avons appliqué des données, combinant des valeurs hypothétiques de C_{max} à des températures extrêmes et nos résultats expérimentaux moyens, à un algorithme utilisable en simulation sur modèle. Autant l'algorithme gamma généralisé que l'algorithme du taux biologique (Thornton et Lessem. 1978. Trans. Am. Fish. Soc. 107 : 284–287) convenaient bien à un modèle hypothétique température–C_{max} sur toute la plage des températures du milieu de 0 à 27°C, observée dans le fleuve Columbia.

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The northern squawfish (*Ptychocheilus oregonensis*) is native to the Columbia River and is a major predator of seaward migrating juvenile salmonids. Such predation is especially high where salmonids are abundant and concentrated (Brown and Moyle 1981), e.g. during hatchery releases (Thompson 1959) and below dams during smolt migration periods (Ebel 1977). In John Day Reservoir, the northern squawfish had the highest rates of salmonid consumption of four major fish predators (Vigg et al. 1991). Northern squawfish was the most abundant piscivore (Beamesderfer and Rieman 1991). The total loss of salmonid juveniles to predation in John Day Reservoir was nearly 3 million fish annually or about 14% of seaward migrants, and northern squawfish accounted for about 78% of the fish predation mortality (Rieman et al. 1991). In comparison, about 2% of the juvenile salmonid population was lost to bird predation at a mid-Columbia dam (Ruggerone 1986). Little is known of the in-river losses of juvenile salmonids due to other mortality agents such as disease, parasitism, and starvation.

The relation between maximum consumption and temperature is fundamental for understanding the predation dynamics of northern squawfish. It is well known that the evacuation rate of northern squawfish increases greatly with increasing temperature (Falter 1969; Steigenberger and Larkin 1974; Beyer et al. 1988). Predator size is another factor that generally affects consumption rates (Brett 1971), and northern squawfish have a piscivorous size threshold. Poe et al. (1991) found that northern squawfish began feeding on salmonids at a length of about 250 mm (about 190 g) and that fish became a major constituent

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of the diet at a length of about 350 mm (about 560 g). However, there are no published studies on the maximum number and ration of salmonids that northern squawfish can consume at various temperatures or predator sizes.

Daily ration is defined as the weight of the daily meal expressed as a percentage of predator body weight, i.e. centigrams per gram per day (Ricker 1946). Maximum consumption (C_{max}) is the physiological maximum daily ration that determines the ultimate upper bound on the growth potential of a fish (Stewart and Binkowski 1986). Quantification of maximum consumption as a function of temperature is prerequisite to modeling predator–prey dynamics when one uses either the bioenergetics approach (Kitchell 1983; Rice et al. 1982) or the empirical approach based on the functional response of predation rate to prey density (Vigg 1988; Beamesderfer et al. 1990).

Our objectives in the present work were to quantify the maximum daily consumption of northern squawfish with respect to temperature and predator size using an empirical model and to develop a hypothetical model of maximum consumption for the entire environmental temperature range of northern squawfish habitats. We fitted our data to various mathematical equations, i.e. exponential, exponential sigmoid, generalized gamma, Thornton and Lessem (1978), and polynomial. We tested a variety of algorithms in order to make comparisons with previous maximum consumption rate studies on other predatory fish species and to evaluate which model would be most suitable for use in northern squawfish dynamic ecosystem models. Maximum consumption of juvenile salmonids was evaluated in terms of number and ration consumed per day by northern squawfish fed to satiation (i.e. the physiological maximum). Comparative data on in situ stomach contents and thermal preference and lethal relations of this predator at the lower and upper extremes were used to hypothesize the probable temperature–consumption relation outside the range of our experimental data.

Materials and Methods

Northern squawfish were collected during April–October 1987 and July–September 1988 from the John Day Reservoir, Columbia River (Fig. 1). The primary collection method was electroshocking from a 6.4-m boat. Northern squawfish were also collected by hook and line from the tailrace of McNary Dam, John Day Reservoir. The thermal history of the habitat sampled was obtained from the records of the U.S. Army Corps of Engineers (B. Eby, U.S. Army Corps of Engineers, Walla Walla District, WA, pers. comm.). Northern squawfish were transported to and maintained at the U.S. Fish and Wildlife Service (USFWS), Columbia River Field Station, Cook, WA. They were fed a maintenance diet of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) reared at the USFWS Little White Salmon - Willard National Fish Hatchery.

Laboratory Facilities

Tests were conducted with 12 circular fiberglass tanks (1365 L) in a recirculating system consisting of a biofilter, sand filter, ultraviolet lights, and thermostatically controlled heaters. General operational procedures were documented by Lucchetti and Gray (1988). The system was contained in a laboratory having air temperature and photoperiod regulation. The annual variation in the temperature of the well-water supply was about 6°C (4–10°C), pH was about 7.0, and total hardness was 20 $mg \cdot L^{-1}$. The proportion of water reused could be varied from 0 to 100% but was below about 10% during our study.

The protocol of the experiments was similar to that summarized by Stewart and Binkowski (1986). Predator weight and temperature were treatments of the experiment that were systematically varied. Characteristics held constant were duration of the feeding experiment (48 h), prey species composition and size range, photoperiod (12:12 h, light–dark), and light intensity (1.5 lx). Both number (six) and individual weight (about 5% coefficient of variation) of northern squawfish per tank were also held constant to standardize feeding behavior.

Tests were designed to encompass the preferred thermal range of northern squawfish that we postulated (10–21°C) and be within the range of temperatures observed in the Columbia River (0–27°C) (USFWS, Columbia River Field Station, unpubl. data). Tests were scheduled for four target temperatures: 8.0, 12.5, 17.0, and 21.5°C (Fig. 2). For this paper, we define "acclimization period" as the 60-d interval in the natural environment preceding the acclimation period and "acclimation period" as the approximately 30-d interval in the laboratory tanks before the test (2-d duration). Actual test temperatures were within 0.4°C of the target temperatures.

To obtain size-specific C_{max} relations, we tested a size range of northern squawfish (Fig. 3A), stratified by weight group. The size of northern squawfish we tested (>500 g) was based on the predator size (350 mm) at which prey fish became predominant in the diet. When possible, four replicates (groups of six fish) of the three following weight ranges were tested at each temperature: 501–1100, 1101–1500, and 1501–2000 g. For each replicate, the total grams of prey consumed per total grams of predator made one observation; thus, each observation represented a mean value for the six fish. Each test group was as uniform in weight as practicable, i.e. the mean coefficient of variation in weight for the 58 test groups was 4.3%.

Because of problems in collecting sufficient numbers of large predators during late summer, we were unable to obtain a balanced experimental design. The number of replicates for each test temperature was stratified by predator size (Table 1). The 17.0°C treatment was repeated in 1988 (experiment 5) because no large fish (>1500 g) were tested in experiment 3. During 1988, we were again unable to collect enough large northern squawfish for a balanced design. However, we used the combined results from both tests at 17.0°C (experiments 3 and 5). Overall, we made five tests at four different temperatures including a total of 58 replicate tests with six predators each.

Test Procedure

Northern squawfish were sorted by weight, and groups of six fish were randomly placed in the 12 tanks and allowed to acclimate to the test temperature for at least 1 mo before the tests. Only healthy, actively feeding fish were used. They were deprived of food for sufficient time to empty the gut, as calculated from a temperature-dependent evacuation rate equation developed by Beyer et al. (1988). During the tests, northern squawfish with initially empty stomachs were fed juvenile coho and chinook salmon of a selected size range (Fig. 3B) at the start, every 4 h during, and near the end of a 48-h period (i.e. 14 feedings). The final feeding was 47.5 h from the start. Prey fish were weighed when they were introduced into the tanks. Those not eaten were weighed at the end of the test (±0.1 g).

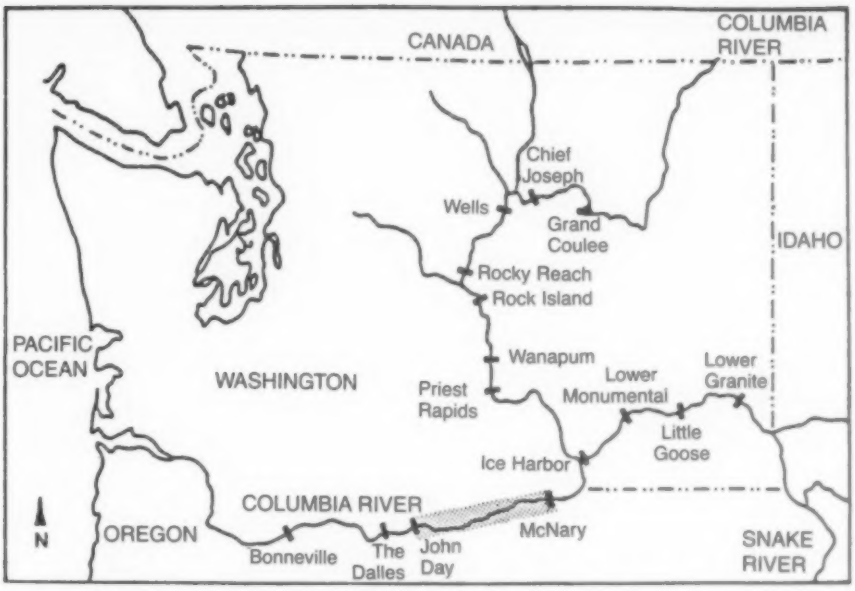

FIG. 1. Location of John Day Reservoir (shaded) in the Columbia River Basin (bars represent dams on the rivers).

Individual northern squawfish weights, minus the weight of stomach contents, were measured (±1 g) at the end of the experiment. Maximum daily ration of the sample was calculated as total weight of prey fish consumed (centigrams) per total predator weight (grams) per 24 h, i.e. centigrams per gram per day.

Water temperature was continuously monitored in each test tank with calibrated recording meters. Dissolved oxygen (milligrams per litre) was measured daily with a calibrated meter. Gross mineral, nutrient, and trace metal analyses were conducted once on the water source before the study, on 9 March 1987.

Empirical Model of C_{max}: Temperature Range 8–21.5°C

The maximum consumption data, within the 8.0–21.5°C range of our experiments, were fitted using regression techniques to two nonlinear functions of temperature. First, an exponential model:

$$(1)\quad C_{max} = ae^{bT}$$

where C_{max} is maximum consumption rate as either daily ration (centigrams per gram) or number consumed (smolts per predator), T is temperature (degrees Celsius), and a and b are empirical constants. Thus, the daily C_{max} is represented as a proportion of predator weight or number consumed per predator, and an exponential function of temperature (Brett 1971; Kerr 1971; Elliot 1976). We used least-squares linear regression with natural log transformations to estimate the coefficients from the data:

$$(2)\quad \ln C_{max} = \ln a + (bT).$$

Second, an exponential sigmoid model was fitted to the data by least-squares nonlinear regression:

$$(3)\quad C_{max} = a/\{1 + be^{(cT)}\}$$

where T is environmental temperature, a is the asymptotic consumption rate, and b and c are empirical constants.

Theoretical Model of C_{max}: Temperature Range 0–27°C

Three different algorithms were used to model C_{max} over the entire temperature range that exists in northern squawfish habitats, i.e. 0–27°C. To model the relations beyond the range of our experimental data, we used the mean values from our experiments at the range of 8–21.5°C and temperature relations (preferred and lethal) observed by other workers and made assumptions about decreasing consumption rates as temperature approached the lower and upper incipient lethal levels, i.e. no consumption at 0–1°C nor at 27–30°C. We also assumed that 21.5°C approximates the optimum temperature for peak consumption. First, we fitted the mean experimental and hypothetical data to the generalized gamma function (L. J. Bledsoe, Center for Quantitative Science, University of Washington, Seattle, WA, pers. comm.):

$$(4)\quad C_{max} = \{(T/T_0)^a\}\{e^{((a/b)(c-((T/T_0)^a b)))}\}$$

where C_{max} is maximum consumption rate as either daily ration (centigrams per gram) or number consumed (smolts per predator) normalized to 1, T is environmental temperature (degrees Celsius), T_0 is the assumed temperature for peak consumption (21.5°C), and a, b, and c are empirical constants.

Second, we used the biological-rate temperature algorithm of Thornton and Lessem (1978):

$$(5)\quad C_{max} = K_A(T)\cdot K_B(T)$$

$$K_A(T) = \frac{K_1 e^{v_1(T-T_1)}}{1 + K_1\{e^{v_1(T-T_1)} - 1\}}$$

$$K_B(T) = \frac{K_2 e^{v_2(T-T_2)}}{1 + K_2\{e^{v_2(T-T_2)} - 1\}}$$

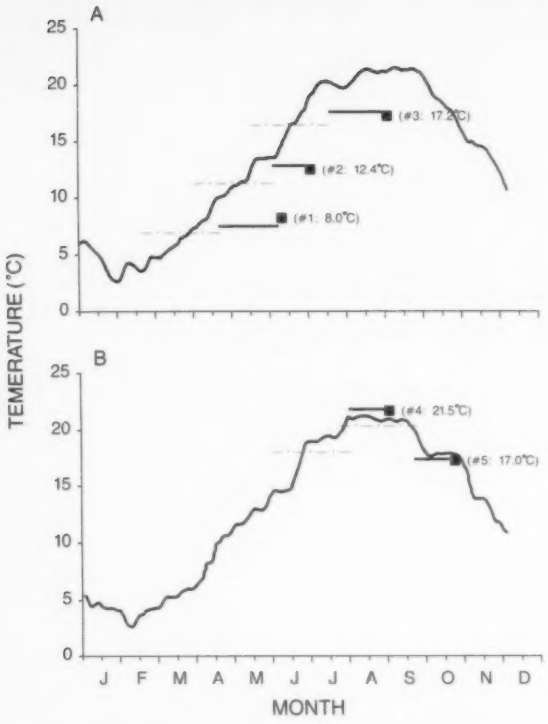

FIG. 2. Experimental temperatures during (A) 1987 and (B) 1988: river water (long solid line), acclimization (dashed-dotted lines), acclimation (short solid lines), and test (solid squares). Mean test temperature values are in parentheses.

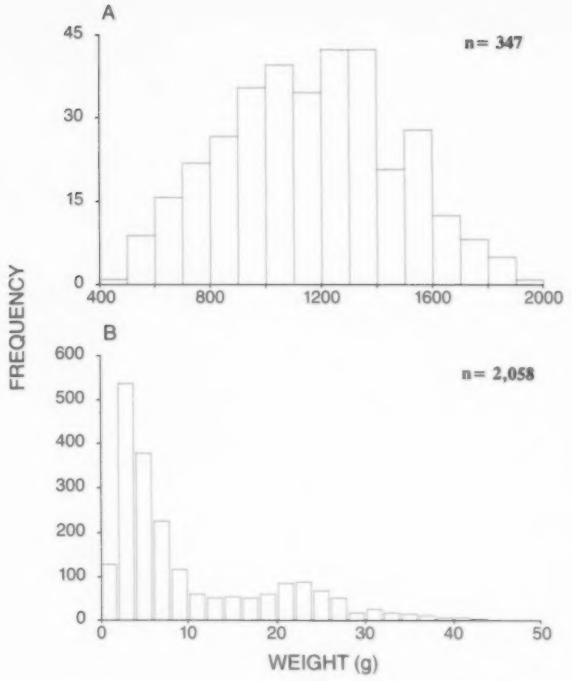

FIG. 3. Size frequency distributions of (A) northern squawfish and (B) juvenile salmon.

where C_{max} is maximum consumption rate normalized to 1, T is environmental temperature (degrees Celsius), T_1 is the temperature at the lower consumption threshold, T_2 is the temperature at the upper consumption threshold, K_1 is the rate multiplier near the lower threshold temperature, K_2 is the rate multiplier near the upper threshold temperature, v_1 is the empirical lower specific rate coefficient, and v_2 is the empirical upper specific rate coefficient (see Thornton and Lessem (1978) for a detailed derivation of coefficients).

Third, we used a polynomial model:

$$(6) \quad C_{max} = a(T)^2 + b(T)^3 + c(T)^4 + d(T)^5 + e(T)^6$$

where T is environmental temperature (degrees Celsius), the y-intercept is zero, and a, b, c, d, and e are empirical constants.

Wet–Dry Weight Relations

Juvenile coho or chinook salmon were randomly collected from each of three size groups (mean weight in parentheses): five small coho salmon (4.3 g), 25 medium chinook salmon (13.3 g), and 30 large coho salmon (26.9 g). Each fish was killed, blotted dry, and weighed to the nearest 0.001 g with an electronic balance. At the end of each test, one northern squawfish from each of the three size groups (i.e. 500–1100, 1101–1500, and >1500 g) was weighed to the nearest gram, labeled, and frozen for later dry weight determination.

The fresh juvenile salmon and the thawed northern squawfish were cut into sections and blended separately to a homogeneous mixture in a commercial blender. The mixture was then reweighed to the nearest 0.001 g before drying. Each blended fish was assigned a separate ceramic crucible and dried at 60°C for at least 6 d or until the weight was constant for three consecutive weighings, whereupon the final dry weight measurement was made. Equations for converting wet to dry weight were calculated by using least-squares linear regressions with y-intercept of zero.

TABLE 1. Number of replicates (six fish per replicate) for each treatment of the maximum consumption experiment.

Predator size group		Test number and temperature (°C)					
Weight (g)	Length (mm)	1 8.0	2 12.5	3 17.0	4 21.5	5 17.0	Sum
501–1100	358–432	4	4	4	6	7	25
1101–1500	433–477	4	4	6	4	5	23
1501–2000	478–522	4	4	0	2	0	10
Total		12	12	10	12	12	58

Results

In all experiments combined, 341 northern squawfish averaging 1148 g consumed 2363 juvenile salmonids averaging 8.0 g; this translates to a maximum daily consumption rate of 2.4 cg·g^{-1} or 3.5 salmonids·predator^{-1}. However, maximum consumption rate was significantly related to temperature and varied somewhat with predator size. The mean maximum daily

TABLE 2. Maximum consumption rates of salmonid prey (mean percent daily ration and number per predator) by northern squawfish predators at different water temperatures. Standard deviations of consumption estimates are in parentheses.

Predator weight (g)	Temperature (°C)	Mean ration ($cg \cdot g^{-1}$)	Number per predator	Number of replicate tests
501–1100	8.0	0.75 (0.67)	0.52 (0.40)	4
	12.5	0.91 (0.39)	1.25 (0.36)	4
	17.0[a]	3.52 (2.14)	4.06 (2.22)	11
	21.5	4.23 (3.24)	6.03 (4.42)	6
1101–1500	8.0	0.27 (0.28)	0.40 (0.40)	4
	12.5	0.70 (0.61)	1.27 (0.99)	4
	17.0[a]	3.25 (1.27)	4.41 (2.30)	11
	21.5	5.42 (1.19)	8.50 (2.43)	4
1501–2000	8.0	0.28 (0.21)	0.46 (0.32)	4
	12.5	0.48 (0.42)	1.00 (0.58)	4
	17.0[a]	—	—	0
	21.5	3.48 (2.95)	7.00 (5.89)	2
Mean of replicate tests[b]	8.0	0.47 (0.46)	0.50 (0.33)	11
	12.5	.70 (0.47)	1.17 (0.64)	12
	17.0	3.39 (1.72)	4.25 (2.19)	22
	21.5	4.50 (2.55)	7.01 (3.87)	12

[a]Mean of two experiments, tests 3 and 5.
[b]Mean of all individual replicate tests per temperature.

ration (centigrams per gram) increased as a function of temperature from about 0.5 at 8.0°C to 4.5 at 21.5°C (Table 2; Fig. 4A). Likewise, the mean number consumed increased from 0.5 at 8.0°C to 7.0 salmonids·predator^{-1} at 21.5°C (Fig. 4B).

Empirical Model of Maximum Daily Ration

The maximum daily ration data versus temperature were fitted to an exponential equation (equation 1):

$$C_{max} = 0.0544\, e^{(0.2095T)}$$

where C_{max} is the maximum daily ration and T is temperature (degrees Celsius). To better describe the known leveling off of maximum daily ration at an optimum temperature, we fitted an exponential sigmoid function to the data (equation 3):

$$C_{max} = 4.7377/\{8.776e^{(-0.5069T)}\}.$$

Coefficients for the temperature models in terms of number of salmonids per predator are given in Table 3.

No significant bivariate relation was observed between northern squawfish weight and replicate C_{max} measurements ($p > 0.05$); however, mean C_{max} generally decreased with increasing predator weight (Fig. 5A). To test the efficacy of a multiple regression approach (e.g. Wootton et al. 1980), we regressed the C_{max} residuals (ration and numbers) from both temperature models (equations 1 and 3) on northern squawfish weights. The inclusion of weight as an additional independent variable did not explain a significant proportion of variability ($R^2 = 0.0003$–0.025).

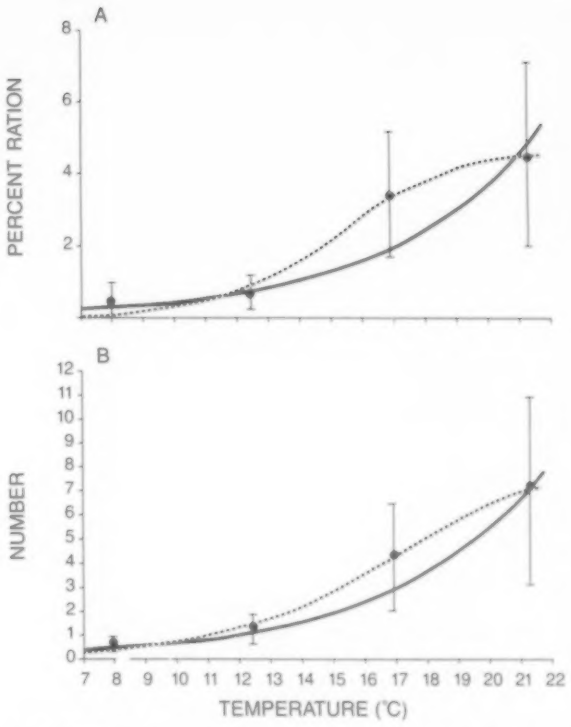

FIG. 4. Maximum consumption of juvenile salmonids by northern squawfish as a function of temperature, fitted to exponential (equation 1, solid line) and exponential sigmoid (equation 3, dotted line) models for (A) daily percent ration and (B) number consumed. Mean values of maximum consumption (solid circles; $n = 11$–22) are bounded by 1 standard deviation (bars).

Theoretical Model of Maximum Daily Ration

Models of generalized gamma (equation 4), the Thornton and Lessem (1978) biological-rate algorithm (equation 5), and the polynomial (equation 6) were fitted to mean maximum consumption rates over the entire environmental temperature range, i.e. 0–27°C (Table 3). These relations were derived from our maximum consumption experiments, a knowledge of in situ consumption rates, the upper thermal relations of northern squawfish, and assumptions of the cessation of feeding at low and high thermal extremes (Fig. 6).

Wet–Dry Weight Relations

The linear regression equations for the combined coho salmon and chinook salmon (equation 7) and the northern squawfish (equation 8) were as follows:

(7) $D_c = 0.218(W_c)$ $(n = 60, R^2 = 0.99)$

(8) $D_s = 0.306(W_s)$ $(n = 12, R^2 = 0.99)$

TABLE 3. Coefficients for five models of maximum consumption rate (ration and number) as a function of temperature.

Model	Equation from text[a]	Coefficients (statistics)	Maximum consumption measure: Ration	Maximum consumption measure: Number
		8–21.5°C		
Exponential	1	a	0.0544	0.0818
		b	0.2095	0.2066
		(n)	57	57
		(R^2)	0.520	0.593
Sigmoid	3	a	4.7377	8.4897
		b	7.7760	6.0781
		c	−0.5069	−0.3545
		(n)	57	57
		(R^2)	0.512	0.535
		0–27°C		
Generalized	4	T_0	21.5	21.5
Gamma		a	2.8227	3.3627
		b	13.7319	13.7628
		(n)	6	6
		(R^2)	0.979	0.997
Thornton and Lessem 1978	5	T_1	0	0
		T_2	27	27
		K_1	0.001	0.001
		K_2	0.01	0.01
		v_1	0.4944	0.4521
		v_2	1.8380	1.8381
		(n)	6	6
		(R^2)	0.965	0.983
Polynomial	6	a	0.05904	0.11405
		b	−0.01735	−0.03209
		c	0.00181	0.00318
		d	−0.00007	−0.00001
		e	9.9×10^{-7}	1.7×10^{-6}
		(n)	6	6
		(R^2)	0.959	0.953

[a]Equations:

Exponential:

$$C_{max} = ae^{bT}$$

Sigmoid:

$$C_{max} = 21.5/\{(1 + b)e^{(-cT)}\}$$

Generalized Gamma:

$$C_{max} = \{(T/T_0)^a\}\{e^{((a/b)(1-((T/T_0)^b)))}\}$$

Thornton and Lessem (1978):

$$C_{max} = K_A(T) \cdot K_B(T)$$

$$K_A(T) = \frac{K_1 e^{v_1(T-T_1)}}{1 + K_1\{e^{v_1(T-T_1)} - 1\}}$$

$$K_B(T) = \frac{K_2 e^{v_2(T-T_2)}}{1 + K_2\{e^{v_2(T-T_2)} - 1\}}$$

Polynomial:

$$C_{max} = a(T)^2 + b(T)^3 + c(T)^4 + d(T)^5 + e(T)^6.$$

where D_c is the dry weight of the combined salmon, W_c is the wet weight of the combined salmon, D_s is the dry weight of the northern squawfish, and W_s is the wet weight of the northern squawfish.

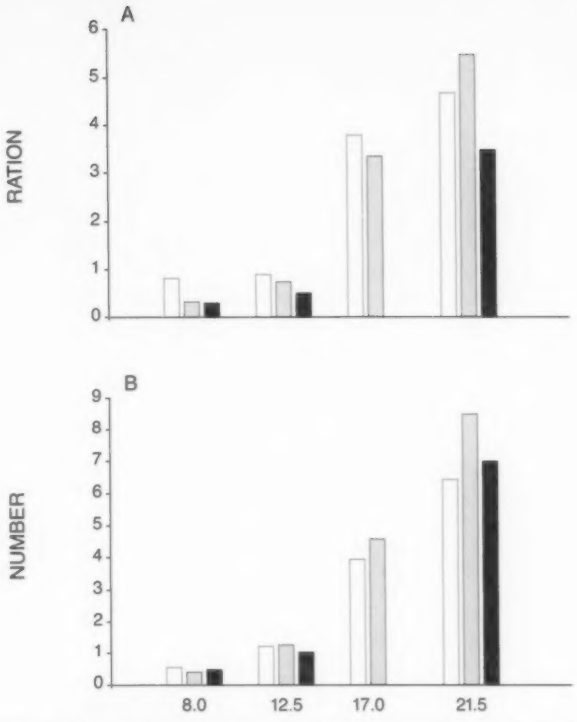

FIG. 5. Maximum consumption of juvenile salmonids by northern squawfish stratified by temperature and predator size group (small, clear; medium, shaded; and large, black) for (A) daily percent ration and (B) number consumed.

Discussion

Empirical Model of Maximum Daily Ration

We found that temperature was the overriding variable affecting the maximum consumption rate of northern squawfish. The exponential sigmoid (equation 3) was the most realistic model of temperature dependency of consumption rate within the tested temperature range because it incorporates the asymptotic C_{max} at high temperatures, i.e. it does not increase without bounds at temperatures above the test range. Based on available temperature relations for northern squawfish (e.g. Black 1953; Dimick and Merryfield 1945; Steigenberger and Larkin 1974), we assumed that the optimum temperature for peak consumption is near the highest temperature we tested (21.5°C), but further work will be required to refine optimum temperatures for consumption and growth.

Insignificant additional variability in C_{max} was explained by including predator weight as a predictor variable. The lack of a significant relation between predator weight and C_{max} may be due to the variability of consumption rate among weight replicates and interactions between temperature and weight effects. Inspection of the graphed data, however, indicates that mean ration generally had the expected decreasing trend with increasing predator weight (Fig. 5A). This size relation, however, was not consistent at all temperatures, i.e. the medium-sized group at 21.5°C was anomalous. Another factor affecting the weight relation in our experiments was the exclusion of small northern squawfish (<500 g); these mostly

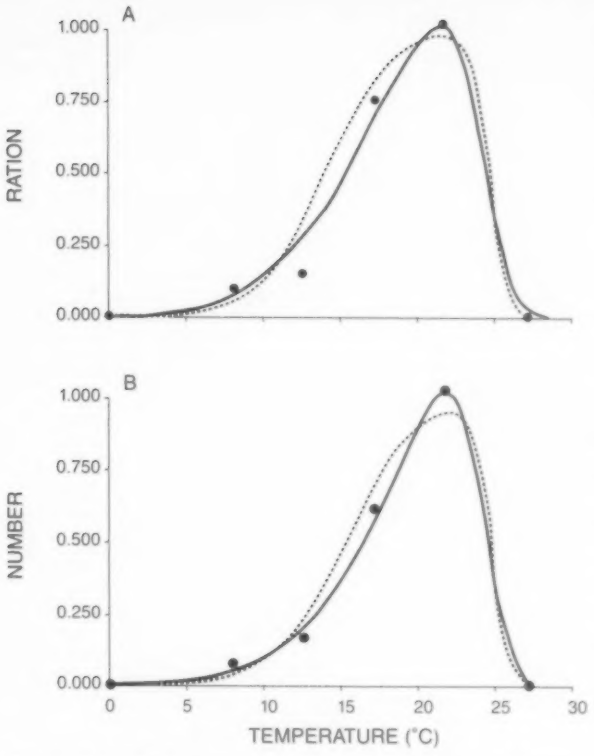

FIG. 6. Generalized gamma (solid line) and Thornton and Lessem (1978) (dotted line) models for maximum consumption in terms of (A) daily ration ($cg \cdot g^{-1}$) and (B) number per predator, normalized to 1.

nonpiscivorous fish may have higher metabolic requirements and thus consume larger daily rations.

Decreasing consumption rate with increasing predator weight is consistent with general theory, but is inconsistent with mean consumption rates observed in John Day Reservoir (Vigg et al. 1991). In that study, observed mean daily ration of northern squawfish increased with predator size. This apparent discrepancy may be explained by the fact that the mean daily ration in John Day Reservoir ($<1.5\ cg \cdot g^{-1}$) was considerably below the physiological rations determined here, and other factors (e.g. food availability and behavioral dominance relations) probably constrain consumption in nature.

Brett (1979) summarized the factors that affect maximum consumption: (1) duration of a given feeding (satiation time), (2) individual meal size (stomach capacity), (3) time between meals (feeding interval), and (4) interaction among the factors. Temperature and consumer size are usually the most important abiotic and biotic determinants of these factors; C_{max} increases with temperature within the range a species normally inhabits and decreases with fish size (Brett 1979). Wootton et al. (1980) presented various models for predicting maximum daily consumption rates of fishes: four models with predator body weight as the independent variable, five models with temperature, and two multivariate (weight and temperature) models. They concluded that a bivariate power model for weight and a multiple regression power model incorporating weight and temperature had the best empirical fits for two species, *Gasterosteus aculeatus* and *Phoxinus phoxinus*. Similarly, Elliott (1975) found that a multivariate (weight and temperature) power relation was an appropriate model for brown trout (*Salmo trutta*). Thus, the conclusions of previous studies on other predaceous fish species are not in agreement with our results which indicated that an exponential sigmoid model (temperature–C_{max}) was most appropriate for northern squawfish within the preferred temperature range.

Theoretical Model of Maximum Daily Ration

Both the biological-rate algorithm (Thornton and Lessem 1978) and the generalized gamma models are suitable to describe maximum consumption rate of northern squawfish as a function of temperature, over the environmental temperature range observed in the Columbia River (0–27°C). The Thornton and Lessem (1978) model has been used for a variety of species, including two species that are predators in John Day Reservoir, i.e. smallmouth bass (*Micropterus dolomieui*) and channel catfish (*Ictalurus punctatus*); therefore, interspecific comparisons in the coefficients and the shape of the curves can be made. The generalized gamma model is a simpler mathematical algorithm, has a slightly better fit to the data, and passes through the data point at peak consumption. Both models provide a reasonable fit to the mean temperature–consumption data ($R^2 > 0.96$) and have coefficients that can be interpreted in terms of biological processes.

Maximum daily ration for many fishes increases with increasing temperature to a maximum near the preferred temperature of the species and declines to near zero just below the maximum lethal temperature (Elliott 1976; Kitchell et al. 1977; Brett 1983; Bevelhimer et al. 1985; Stewart and Binkowski 1986). The survival of northern squawfish (percent) was 100 at 26.4°C, 50 at 29.3°C, and 0 at 32.0°C for fish acclimated at 18.9–22.2°C (Black 1953). Thus the incipient upper lethal temperature is about 29°C (Brown and Moyle 1981). Based on field observations, northern squawfish prefer temperatures of about 16–22°C (Dimick and Merryfield 1945). Northern squawfish digested fish at rates of 5, 14, and 40–50%·h^{-1} at temperatures of 4–6, 10–12, and 24°C, respectively (Steigenberger and Larkin 1974). Falter (1969) and Beyer et al. (1988) also observed acceleration in digestion rate with temperature. From these data, we predict that temperature-specific C_{max} will be near zero at 0°C, very low at 4°C, will peak at 20–24°C and will be near zero at 27°C. Temperature of McNary Dam discharge ranges from about 0.5 to 23.5°C; subsurface temperatures measurements in the reservoir were significantly higher, especially in backwater areas (about 27°C).

The polynomial equation (6) had the lowest fit (R^2), over the entire environmental temperature range, of the three models of northern squawfish maximum consumption rate. Diana (1987) used a multivariate model for maximum consumption rate of northern pike (*Esox lucius*) that incorporated a power function of predator weight and a polynomial function of temperature. We do not consider the polynomial model valid because it has the undesirable characteristics of being purely empirical with no underlying theoretical basis, of having coefficients with no biological meaning, and of exhibiting unrealistic cyclic behavior at the lower and upper extremes.

We analyzed the relation between temperature and C_{max} both in terms of daily ration and number of salmon consumed per northern squawfish. In applying our results to predation models, we believe that the use of ration as the measure of C_{max} is usu-

ally more appropriate because it standardizes the weight of salmonid prey consumed per unit weight of predator. In nature, where both the size of predator and prey vary substantially on a seasonal or spatial basis, erroneous predictions of C_{max} could be derived if number were used as the criterion variable (unless the mean weights of the northern squawfish and salmonid prey were very similar to those of our test fish). For example, extremely high numbers of salmon fry ($>200 \cdot \text{predator}^{-1}$) have been observed in the stomachs of northern squawfish in a backwater below Little White Salmon Hatchery near Cook, WA (USFWS, unpubl. memorandum, 1951). Our results are presented in wet weight; however, for greater utility, we present conversion factors of wet to dry weight for both adult northern squawfish and juvenile salmon.

Both the functional response relation (Vigg 1988) and maximum consumption rate relation are central to prototype predation simulation models for the John Day Reservoir (Beamesderfer et al. 1990) and the Columbia River System (L. J. Bledsoe, Center for Quantitative Science, University of Washington, Seattle, WA, pers. comm.). Modeling predator–prey dynamics may be the only practical way to quantify the system-wide losses to predators and for understanding the factors affecting predation in a river as large and perturbed as the Columbia.

Acknowledgements

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Characteristics and Function of Large Woody Debris in Streams Draining Old-Growth, Clear-Cut, and Second-Growth Forests in Southwestern Washington

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Bilby, R. E., and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Can. J. Fish. Aquat. Sci. 48: 2499–2508.

Amount of large woody debris (LWD) surveyed in 70 stream reaches flowing through old-growth, clear-cut, and second-growth forests decreased with increasing stream size for all stand types but was greatest at old-growth sites. Average piece volume was larger at old-growth sites than at other stand types in streams >10 m wide, but no differences were seen in smaller streams. Scour pools accounted for 90% of the wood-associated pools at second-growth and clear-cut sites but only 50% at old-growth sites, which contained more pools than other stand types, particularly for larger streams. Pool size was similar for all stand types in smaller streams, but averaged 10 m^2 in streams >10 m wide at old-growth sites and 4 m^2 for other stand types. Pool size was similar for all stand types in smaller streams. Sediment and fine organic matter retained by woody debris decreased with increasing stream size for all stand types, but old-growth sites contained greater amounts of both materials than other stand types. The frequency of pool formation, the type of pool formed, and sediment accumulation were influenced by the amount of fine debris associated with LWD. Changes in LWD amount, characteristics, and function occurred very rapidly following removal of streamside vegetation.

Les quantités de gros débris ligneux (GDL), étudiées dans 70 tronçons de cours d'eau s'écoulant dans de vieilles forêts, des forêts coupées à blanc et des forêts de seconde venue, ont diminué en fonction de l'augmentation de la taille des cours d'eau dans tous les types de peuplements, mais ce sont les vieilles forêts qui ont donné lieu aux quantités de GDL les plus importantes. Le volume moyen des débris présents dans les cours d'eau d'une largeur supérieure à 10 m a également été plus grand dans les vieilles forêts que dans les autres sites, mais dans le cas des cours d'eau plus étroits, on n'a pas observé de différence entre les trois types de peuplements. Les zones calmes d'affouillement représentaient plus de 90 % des zones calmes formées par les débris de bois dans les forêts de deuxième venue et les forêts coupées à blanc, mais seulement 50 % dans les vieilles forêts, qui comptent un plus grand nombre de zones calmes que les autres types de peuplements, surtout en ce qui a trait aux cours d'eau plus larges. La taille des zones calmes dans les petits cours d'eau était semblable dans tous les types de peuplements, alors que dans les cours d'eau de plus de 10 m de largeur, elle était en moyenne de 10 m^2 dans les vieilles forêts et de 4 m^2 dans les autres peuplements. Les sédiments et les matières organiques fines retenus par les débris ligneux ont diminué en fonction de l'augmentation de la largeur du cours d'eau dans tous les sites; toutefois, les vieilles forêts contenaient de plus grandes quantités de ces deux matériaux que les autres sites. La quantité de débris accompagnant les GDL a influé sur la fréquence de formation des zones calmes, le type de zones calmes et l'accumulation de sédiments. Des modifications de la quantité de GDL ainsi que de leurs caractéristiques et de leur rôle sont apparues très rapidement après l'élimination de la végétation riparienne.

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Large woody debris (LWD) controls many of the structural and functional properties of smaller streams in forested areas (Bilby and Likens 1980; Harmon et al. 1986; Bisson et al. 1987; Bilby and Ward 1989). Wood affects channel form through the formation and stabilization of pools, waterfalls, and gravel bars (Heede 1972; Bilby 1981; Lisle and Kelsey 1982; Lisle 1986). LWD influences sediment routing through the formation of depositional sites and the creation of waterfalls, which reduce the efficiency of downstream transport of particulate materials (Heede 1972; Swanson and Lienkaemper 1978; Beschta 1979; Bilby 1981; Megahan 1982). A large proportion of the standing stock of particulate organic matter in streams is often associated with LWD (Naiman and Sedell 1979; Bilby and Likens 1980). Wood also provides habitat for some invertebrates (Benke et al. 1984) and fishes (Bustard and Narver 1975; Bisson et al. 1982; Tschaplinski and Hartman 1983; Dolloff 1986; Elliott 1986; McMahon and Hartman 1989).

Features of the stream channel and the bordering riparian vegetation influence the amount and function of LWD. Channel size affects both wood amount and the relative influence of LWD on channel features (Swanson et al. 1976; Bilby 1979; Long 1987; Bilby and Ward 1989). Density of streamside trees is positively correlated with LWD amounts in some systems (Long 1987; Bilby and Wasserman 1989). Morphology of the bed may also influence LWD amount (Bilby and Wasserman 1989). Susceptibility of riparian trees to windthrow can play

a major role in determining quantities of LWD in streams (Lienkaemper and Swanson 1987; Robison and Beschta 1990).

Various management activities in and adjacent to the channel have also influenced LWD amounts and characteristics in Pacific Northwest streams. Removal of wood from rivers for navigation or to provide upstream access for anadromous fishes has greatly reduced LWD amounts in some systems (Sedell and Luchessa 1982; Bilby 1984). Use of splash dams for log transport, a practice which was used widely in the Pacific Northwest until the 1950s, also reduced wood amounts in many streams (Wendler and Deschamps 1955). Removal of streamside timber during logging occurred until the early 1980s in the Pacific Northwest. While this practice no longer occurs, there are many streams where amount of LWD and the composition and structure of the riparian vegetation were influenced as a result of this activity.

Several conceptual models of the influence of streamside timber removal on amount of LWD have been developed (Swanson and Lienkaemper 1978; Likens and Bilby 1982; Grette 1985; Murphy and Koski 1989). In general, these models predict a decrease in LWD over time as a result of decay of wood present in the channel prior to disturbance coupled with decreased input from the riparian area.

Relatively few data have been collected to validate these models. Comparisons of the amount of LWD in streams flowing through old-growth and previously logged forests in several areas in the Pacific Northwest have verified the decrease in wood after removal of the streamside vegetation (Grette 1985; Long 1987). Some information is also available on the influence of stream size and channel characteristics on the rate of change in LWD amount after removal of streamside vegetation (Long 1987; Murphy and Koski 1989). However, little is known about the changes in the characteristics of pieces of LWD or their function over time after removal of streamside vegetation or the rate at which these changes occur. The purpose of this study was to compare LWD abundance, characteristics, and function in streams bordered by forests of differing ages: old-growth forest, recently clear-cut areas, and 40- to 60-yr-old second-growth forest. Comparison of the three stand age-classes provides an indication of the rate at which changes in LWD occur following timber removal from the riparian area.

Description of Study Sites

Measurements of LWD abundance, characteristics, and associated channel features were made on 70 stream reaches in southwestern Washington. All sites were located in the foothills of the Cascade Range or the Willapa Hills. Streams ranged from second order to fifth order with drainage areas from 0.4 to 137 km^2. Bankfull channel widths ranged from 3.1 to 23.5 m. All stream reaches surveyed drained watersheds underlain with volcanic bedrock (Huntting et al. 1961).

One of the most important factors in selection of the sites was the condition of the vegetation adjacent to the surveyed reach. Three stand-age classes were examined: (1) undisturbed, old-growth forest, (2) clear-cut to the channel's edge within 5 yr of the survey, and (3) second-growth forest which had been clear-cut to the edge of the channel 40–60 yr prior to our survey. The clear-cut and second-growth classes had been logged only once.

Sites where factors other than stream size and vegetative characteristics of the riparian zone were likely to have influenced LWD were not surveyed. Stream reaches which had been splash dammed at some time in the past were excluded (Wendler and Deschamps 1955). In addition, streams flowing through clear-cut areas which exhibited evidence of post-harvest channel cleaning were avoided, although selective removal of merchantable wood from the stream during or after logging could not be detected. We also avoided reaches which showed evidence of being influenced by landslides or debris torrents during the recent past.

Mean annual precipitation at the sites varied from 180 to 280 cm, primarily as a result of changes in elevation (Sternes 1969). However, all sites were located within 100 km of one another and thus were likely exposed to a relatively similar history of high discharge events, which play a major role in determining LWD distribution (Bilby 1984; Lienkaemper and Swanson 1987).

Methods

Aerial photographs were utilized to identify streams bordered by appropriate forest conditions. These sites were then examined on the ground to determine if they met the criteria outlined above. Once sites were located, watershed area above the surveyed reach was determined from U.S. Geological Survey topographic maps (scale 1:62500). Additional detail on the techniques employed in this study may be found in Bilby and Ward (1989).

We defined LWD as any piece of wood larger than 10 cm in diameter and 2 m long. Organic material not qualifying as LWD by this definition was considered fine organic debris.

All pieces of LWD within the bankfull channel of the surveyed stream reaches were measured with the exception of those pieces which were either floating free in the channel or resting in an unstable position atop a LWD accumulation. These pieces were considered to have a minimal impact on the channel form or stream function and thus were omitted. However, these pieces were rare and nearly all pieces meeting our size criteria were included in the survey.

We attempted to measure at least 50 pieces of wood at each study site. However, LWD was rare at some of the sites and riparian stand conditions changed before 50 pieces were encountered. Due to our criterion of 50 pieces of LWD per site, the length of stream channel surveyed varied with changing LWD abundance, ranging from less than 100 m to nearly 1.5 km.

Characteristics of the LWD pieces which were measured included diameter, taken at the center of the piece, length in and out of the channel, and the species of tree that produced the piece. Advanced decay prevented identification of species for about 10% of the surveyed pieces. Channel characteristics associated with LWD which were measured included surface area of pools, surface area of sediment accumulations, height of waterfalls, and volume of fine organic debris (organic material less than 10 cm in diameter and 2 m in length, including twigs, leaves, needles, etc.).

Average size of LWD pieces was compared between sites with a debris volume index (Bilby and Ward 1989). This variable was calculated by determining the geometric mean diameter and geometric mean total length (both in and outside the channel) for debris pieces in each surveyed reach. Frequency distributions of LWD diameters and lengths were skewed heavily towards smaller size classes; thus, a geometric mean was used to calculate average values for these variables (Bilby and Ward 1989). The debris volume index is the volume of a cyl-

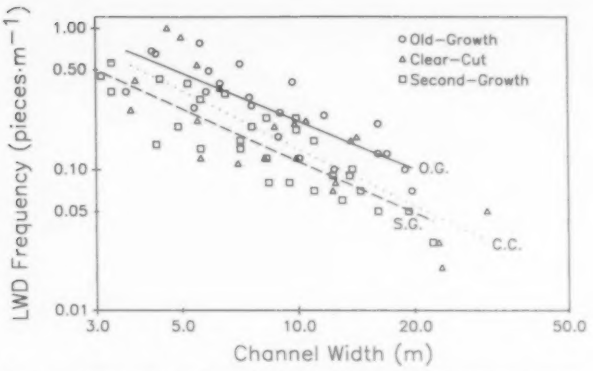

FIG. 1. Relationship between numbers of pieces of LWD per length of surveyed channel and channel width for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the slope values (ANOVA; $p < 0.05$). Equations for the regressions are as follows: old-growth, $\log_{10}$ LWD frequency = $-1.12 \log_{10}$ channel width + 0.46 ($r^2 = 0.69$); clear-cut, $\log_{10}$ LWD frequency = $1.35 \log_{10}$ channel width + 0.50 ($r^2 = 0.66$); second-growth, $\log_{10}$ LWD frequency = $-1.23 \log_{10}$ channel width + 0.28 ($r^2 = 0.75$).

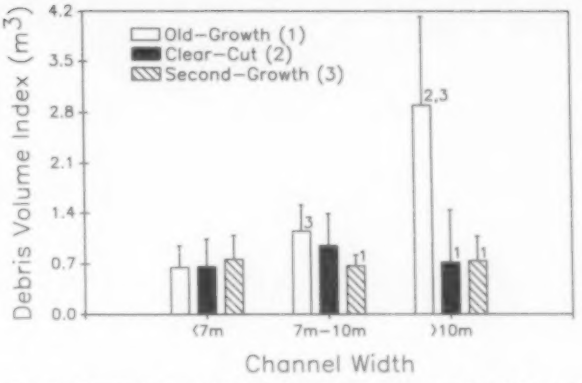

FIG. 2. Comparison of debris volume index (see text for definition) between stand-age classes for channels <7, 7–10, and >10 m wide. Numbers above the bars indicate significant differences from other stand-age classes (t-test; $p < 0.05$).

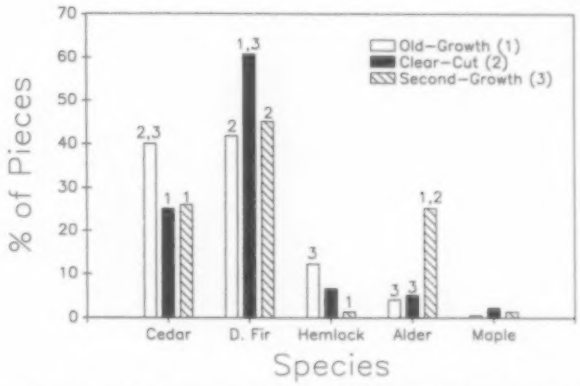

FIG. 3. Species distribution of pieces of LWD in the three stand-age classes. Values significantly different (t-test; $p < 0.05$) from corresponding values for different stand-age classes are denoted with a number above the bar. Cedar = western redcedar (*Thuja plicata*), D. Fir = Douglas fir (*Pseudotsuga menziesii*), Hemlock = western hemlock (*Tsuga heterophylla*), Alder = red alder (*Alnus rubra*), Maple = bigleaf maple (*Acer macrophyllum*).

inder with dimensions equal to the geometric mean diameter and length for each reach.

LWD-associated pools were assigned to one of four classes based on their morphology and method of formation (Bisson et al. 1982). The four classes we recognized were scour pools, plunge pools, backwater pools, and dammed pools.

The influence of fine organic debris on LWD function was examined by comparing the proportion of pieces of LWD retaining large amounts of fine debris (≥ 0.5 m^3) associated with pools, waterfalls, and sediment accumulations with the proportion of pieces of LWD retaining lesser amounts of fine debris associated with these channel features. The same comparison was made between the different pool types to determine if the presence of fine debris favored the formation of certain kinds of pools.

The amount, characteristics, and function of LWD change with changing stream size (Bilby and Ward 1989). Thus, stream size had to be considered in comparing LWD features and function between the three stand-age classes. Because of the variation in precipitation between the study sites, channel width, rather than watershed area, was used as an index of relative stream size.

Regression of LWD features or function against channel width was used for some of the analyses in this study. In cases where regression techniques were not used, streams were segregated into three channel-width classes: <7 m, 7–10 m, and >7 m. There were about an equal number of sites in each stream-size class for each stand-age class. Statistical comparisons of percentage values between stand-age classes and stream-size classes were made using a t-test for equality of two percentages (Sokal and Rohlf 1969).

Results

Abundance, Size, and Species

LWD abundance decreased with increasing stream size for all three stand-age classes (Fig. 1). However, old-growth sites had more wood than similarly sized streams at second-growth or clear-cut sites (t-test; $p < 0.05$). The frequency of LWD pieces in clear-cut and second-growth sites was 59 and 50%, respectively, of that measured in old-growth sites for streams at 15 m wide. In channels 5 m wide, LWD frequency in clear-cut and second-growth sites was 77 and 56%, respectively, of that seen at old-growth sites.

Debris volume index increased with increasing stream size at the old-growth sites (Fig. 2). However, no relationship between piece size and stream size was observed for clear-cut or second-growth sites. The debris volume index for old-growth sites was about four times greater than the other two stand-age classes for streams >10 m wide (ANOVA; $p < 0.05$). LWD piece size was also significantly greater at old-growth sites than at second-growth sites in channels 7–10 m wide. No statistical differences in piece size were observed between stand-age classes for streams <7 m wide.

There were significant differences between stand-age classes in the species distribution of the LWD (Fig. 3; t-test; $p < 0.05$).

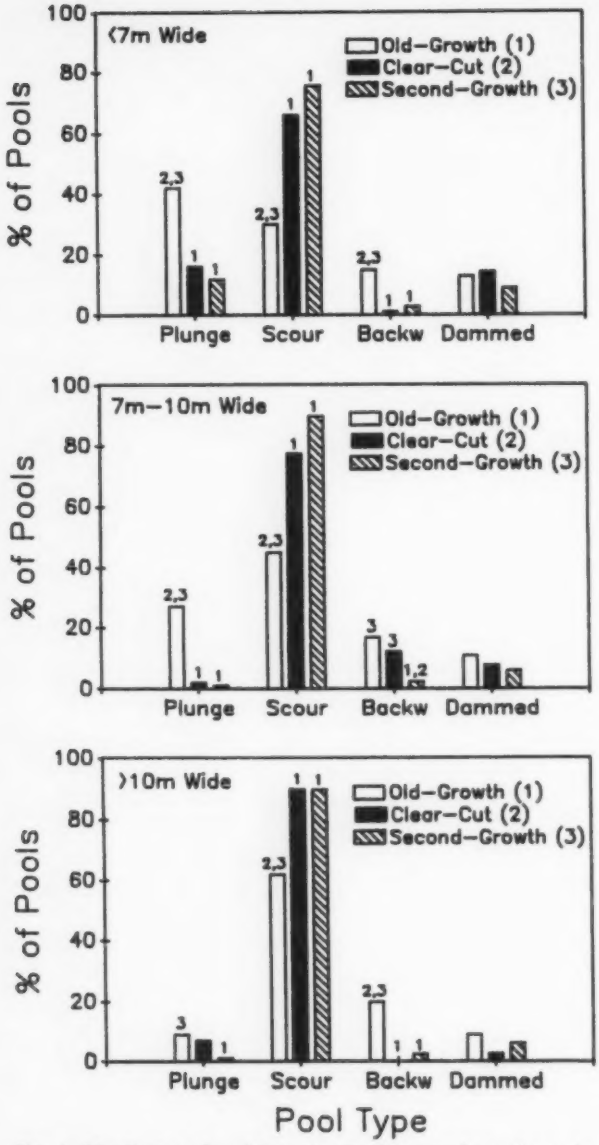

FIG. 4. Distribution of pool types for the three stand-age classes in each of the channel-width classes. Values significantly different (t-test; $p < 0.05$) from corresponding values for other stand-age classes are denoted with a number above the bar.

Western redcedar accounted for 40% of the debris pieces in the old-growth systems but contributed significantly lower proportions of LWD to clear-cut and second-growth sites. Douglas fir, the most commonly encountered species in all stand-age classes, contributed significantly more pieces of LWD in clear-cut systems than in the other two stand-age classes. The proportion of western hemlock was relatively low and progressively decreased from old-growth to clear-cut to second-growth sites. Red alder contributed significantly more pieces of LWD to second-growth sites than to old-growth or clear-cut sites. No differences were observed by stand-age class in the proportion of LWD contributed by bigleaf maple.

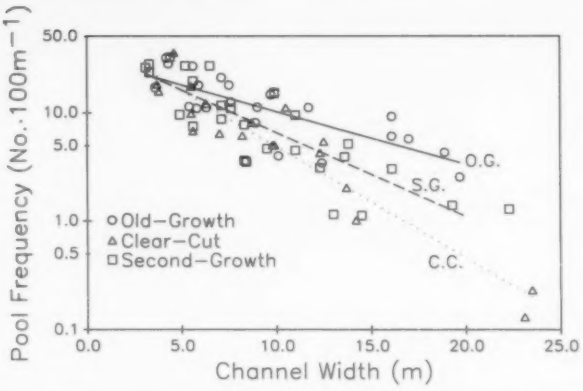

FIG. 5. Relationship between channel width and frequency of LWD-associated pools for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the slope values (ANOVA; $p < 0.05$). Regression equations are as follows: old-growth, $\log_{10}$ pool frequency = -0.05 channel width + 1.49 ($r^2 = 0.64$); clear-cut, $\log_{10}$ pool frequency = -0.10 channel width + 1.71 ($r^2 = 0.90$); second-growth, $\log_{10}$ pool frequency = -0.08 channel width + 1.59 ($r^2 = 0.70$).

However, this species did not produce more than 5% of the wood in any of the stand-age classes.

Pools

The frequency of occurrence of different types of pools associated with LWD changed with stand-age class and stream size (Fig. 4). Pool types were the most diverse in streams bordered by old-growth forest. In these systems, scour pools increased and plunge pools decreased in abundance with increasing stream size (t-test; $p < 0.05$). Scour pools occurred significantly more frequently in clear-cut and second-growth systems than at old-growth sites for all three stream-size classes and were the predominant pool type in all stream-size classes at clear-cut and second-growth sites. Plunge pools formed by LWD were significantly more common at old-growth sites than at second-growth sites for all stream-size classes and at clear-cut sites in streams <7 m wide.

Backwater and dammed pools formed by LWD occurred less frequently than other pool types in all stand-age classes (Fig. 4). Backwater pools were more common at old-growth sites than at second-growth sites for all stream-size classes and at clear-cut sites for streams <7 m wide and >10 m wide (t-test; $p < 0.05$).

Frequency of LWD-associated pools decreased with increasing stream size for all three stand-age classes (Fig. 5) but was significantly greater at old-growth sites than at the other two stand-age classes (t-test; $p < 0.05$). Pool frequency was most similar among stand-age classes in smaller streams. Differences increased with increasing stream size, and frequency of pools associated with LWD in old-growth sites was more than twice that of second-growth sites and three times that of clear-cut sites for streams 15 m wide.

Surface area of debris-associated pools was not significantly different among the stand-age classes for streams <7 m wide or 7–10 m wide (Fig. 6). However, average pool surface area was significantly greater in streams >10 m wide at old-growth sites (t-test; $p < 0.05$), averaging more than twice the area of pools in clear-cut and second-growth systems.

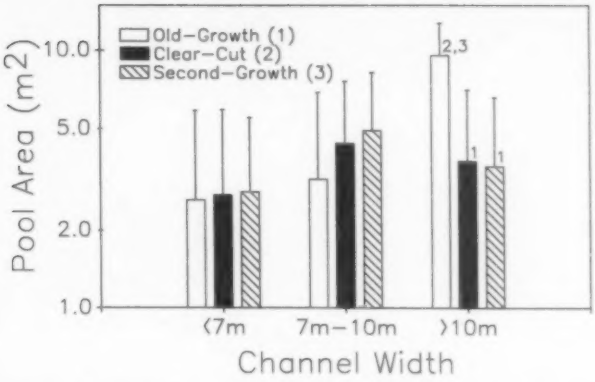

FIG. 6. Comparison of average surface area of scour pools between stand-age classes for different channel widths. Error bars indicate standard deviation. Values significantly different (t-test; $p < 0.05$) from corresponding values in other stand-age classes are denoted with a number above the bar.

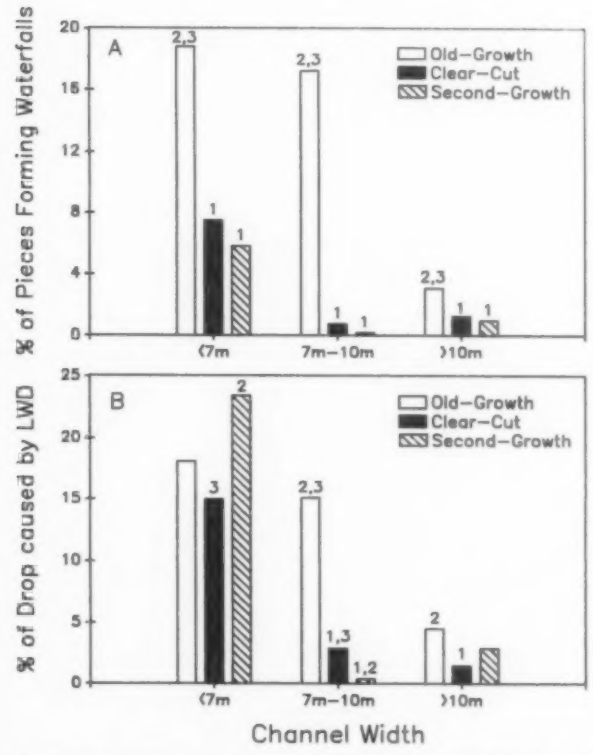

FIG. 7. (A) Proportion of pieces of LWD forming waterfalls and (B) proportion of the total drop in elevation of the surveyed stream sections accounted for by the summed height of LWD-formed waterfalls for the three age classes for each channel-width class. Values significantly different (t-test; $p < 0.05$) from corresponding values in other stand-age classes are denoted with a number above the bar.

Waterfalls

The proportion of pieces of LWD forming waterfalls was significantly greater at old-growth sites than at the other two stand-age classes for all stream-size classes (Fig. 7A; t-test; $p < 0.05$). The proportion of pieces forming waterfalls was greater in streams <7 m wide than in larger systems for all three stand-age classes (t-test; $p < 0.05$).

The proportion of the drop in elevation of a stream reach accounted for by summing the heights of waterfalls formed by LWD decreased with increasing stream size (Fig. 7B). Old-growth sites displayed a greater cumulative elevation drop caused by LWD than the other stand-age classes in streams 7–10 m wide and greater than the clear-cut sites in channels >10 m wide (t-test; $p < 0.05$).

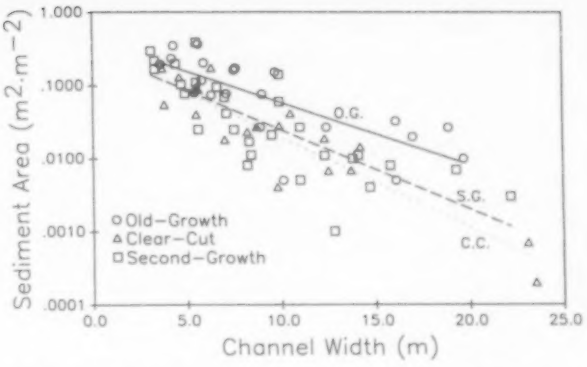

FIG. 8. Relationship between channel width and the surface area of the streambed occupied by LWD-associated sediment accumulations for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the intercept values (ANOVA; $p < 0.05$). Regression equations are as follows: old-growth, $\log_{10}$ sediment area = −0.08 channel width − 0.38 ($r^2 = 0.53$); clear-cut, $\log_{10}$ sediment area = −0.12 channel width − 0.47 ($r^2 = 0.84$); second-growth, $\log_{10}$ sediment area = −0.11 channel width − 0.53 ($r^2 = 0.62$).

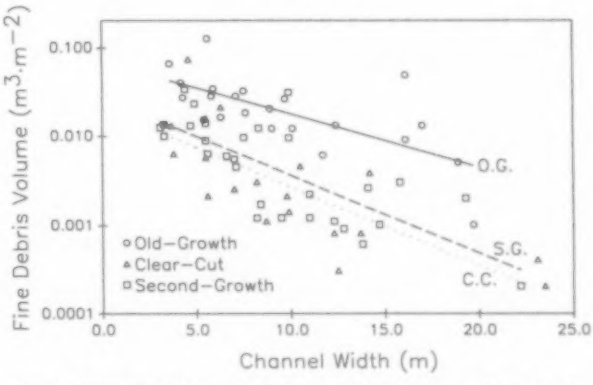

FIG. 9. Relationship between channel width and volume of fine debris associated with LWD for the three stand-age classes (O.G. = old-growth, C.C. = clear-cut, S.G. = second-growth). There are significant differences among the intercept values (ANOVA; $p < 0.05$). Regression equations are as follows: old-growth, $\log_{10}$ sediment volume = −0.06 channel width −1.16 ($r^2 = 0.48$); clear-cut, $\log_{10}$ volume = −0.09 channel width −1.70 ($r^2 = 0.59$); second-growth, $\log_{10}$ volume = −0.09 channel width −1.57 ($r^2 = 0.57$).

Sediment

Proportion of the streambed covered by sediment stored by LWD decreased with increasing stream size for all three stand-

TABLE 1. Proportion of pieces of LWD retaining <0.5 and ≥0.5 m^3 of fine debris associated with pools. Values are significantly different for all stand-age classes (*t*-test; $p < 0.05$).

	Pieces of LWD retaining <0.5 m^3		Pieces of LWD retaining ≥0.5 m^3	
	% forming pools	*N*	% forming pools	*N*
Old-growth	21	881	60	221
Clear-cut	28	858	82	51
Second-growth	39	1346	89	95

age classes (Fig. 8). Area of LWD-associated sediment was greater at old-growth sites than at the other two stand-age classes for all stream sizes (*t*-test; $p < 0.05$). Differences in this variable among the stand-age classes increased with stream size, with an estimated 16, 8, and 9% of the bed surface covered with LWD-associated sediment in channels 5 m wide at old-growth, clear-cut, and second-growth sites, respectively, compared with 2.5, 0.5, and 0.7% in channels 15 m wide.

Fine Organic Debris

The volume of fine organic debris per square metre of channel surface area decreased with increasing stream size for all stand-age classes (Fig. 9), but more fine debris was retained by LWD at old-growth sites than at the other two stand-age classes (*t*-test; $p < 0.05$). Volume of fine organic debris stored by LWD in channels 5 m wide was estimated at 0.035, 0.007, and 0.010 $m^3 \cdot m^{-2}$ at old-growth, clear-cut, and second-growth sites, respectively. The corresponding values for a 15-m-wide channels were 0.0087, 0.0010, and 0.0013 $m^2 \cdot m^{-3}$, respectively.

Fine Organic Debris and LWD Function

Differences between stand-age classes in the frequency of debris-associated pools (Fig. 5) were partly due to a greater amount of fine debris at old-growth sites, although the relative abundance of LWD also was an important factor. In all stand-age classes, pools were associated with pieces of LWD retaining ≥0.5 m^3 of fine debris significantly more frequently than with LWD retaining <0.5 m^3 of fine debris (Table 1; *t*-test; $p < 0.05$). About 20% of the pieces of LWD at the old-growth sites had fine debris accumulations ≥0.5 m^3 compared with 6% at clear-cut and 7% at second-growth sites.

The increased diversity of pool types observed at the old-growth sites may have been related to the large amount of fine organic debris at these sites (Table 2). Plunge and dammed pools were associated with accumulations of fine debris ≥0.5 m^3 significantly more frequently than scour pools in all three stand-age classes (*t*-test; $p < 0.05$). Both plunge pools and dammed pools tend to be formed by obstructions that completely span the channel (Bilby and Ward 1989). Fine debris fills in the gaps in the framework provided by the LWD, resulting in more efficient blockage of stream flow. Since larger fine debris accumulations were rare at clear-cut and second-growth sites (Table 1), it is not surprising that plunge pools were rare and scour pools comprise the vast majority of pools in these systems.

Amount of fine organic debris associated with LWD also may have influenced the formation of depositional sites. LWD with fine debris accumulations ≥0.5 m^3 retained sediment significantly more frequently than LWD pieces with less fine debris (Table 3; *t*-test; $p < 0.05$). Thus, accumulations of sediment associated with LWD were more frequent at old-growth sites due to both high levels of LWD and large amounts of fine debris.

TABLE 2. Proportion of the different pool types associated with fine debris accumulations ≥0.5 m^3. Significant differences between pool types within a stand-age class are indicated with a letter (*t*-test; $p < 0.05$; s = scour pools, p = plunge pools, b = backwater pools, d = dammed pools).

	Pool type			
	Scour	Plunge	Backwater	Dammed
Old-growth				
≥0.5 m^3 (%)	36	49	33	56
Sign. diff.	p, d	s, b	p, d	s, b
N	131	88	58	41
Clear-cut				
≥0.5 m^3 (%)	8	37	33	35
Sign. diff.	p, b, d	s	s	s
N	216	27	12	31
Second-growth				
≥0.5 m^3 (%)	12	26	13	41
Sign. diff.	p, d	s	d	s, b
N	510	31	15	51

Discussion

Effect of Riparian Timber Harvest on LWD

Reduction in LWD amount and piece size as a result of timber harvest has generally been assumed to occur gradually due to a decrease in LWD input coupled with decomposition of material in the channel. However, our data indicate that many changes in LWD abundance, characteristics, and function occur during or shortly after timber harvest. During the 5-yr period separating our old-growth and clear-cut sites, wood amount decreased, average piece size in channels >10 m wide decreased, and the species mix of the LWD changed. It is unlikely that these changes could be attributed solely to decomposition of residual LWD and reduced LWD input over this short time period. The decrease in abundance of large, redcedar logs between the old-growth and clear-cut sites suggests that selective removal of this material from the channel during or shortly after logging may have been a factor in the reduction in LWD. Salvage of redcedar after timber harvest is a common practice in the Pacific Northwest. Removal of LWD from streams also has been shown to destabilize wood remaining in the channel (Bilby 1984), thus promoting flushing of wood downstream and contributing to the decrease in LWD amount. Selective removal of larger logs from channels may also be partly responsible for the lack of relationship between stream size and debris volume index at clear-cut sites. However, since no records of wood salvage from stream channels are kept, the extent to which this practice occurred on our study sites cannot be determined.

Changes in LWD characteristics from the clear-cut to second-growth conditions likely reflect decomposition of residual wood in the channel coupled with reduced input and a change in the composition of the riparian vegetation. The progressive decrease in western hemlock abundance with time after harvest

TABLE 3. Proportion (%) of the pieces of LWD containing fine debris accumulations ≥0.5 and <0.5 m^3 associated with depositional sites. Pieces of wood with large fine debris accumulations are significantly more likely to be associated with areas of deposited sediment in all cases (*t*-test; $p < 0.05$).

	Channel width					
	<7 m		7–10 m		>10 m	
	≥0.5 m^3	<0.5 m^3	≥0.5 m^3	<0.5 m^3	≥0.5 m^3	<0.5 m^3
Old-growth	69.0	30.1	63.8	20.1	36.9	11.9
Clear-cut	60.0	19.7	66.7	16.5	46.2	17.2
Second-growth	64.7	36.9	57.5	20.9	58.1	18.3

indicates elimination of this species from the system without replacement. Since hemlock is less decay resistant than many other conifer species, reduction in its abundance should occur relatively rapidly. The increase in red alder debris in streams in second-growth sites is due to the abundance of this species at the second-growth sites.

There were very large differences between stand-age classes in the amount of fine debris stored by LWD, with old-growth sites containing more fine debris than the other two stand-age classes. Three factors contributed to the large amount of LWD-associated fine debris at the old-growth sites: abundant LWD to retain fine organic matter, a high rate of input from the terrestrial system (Gregory et al. 1987), and high proportions of debris from decay-resistant coniferous trees (Harmon et al. 1986). In contrast, the clear-cut sites have less LWD, very low contributions of organic matter from the terrestrial system, and a high proportion of material from deciduous trees or herbaceous vegetation, which decomposes rapidly. The second-growth sites have conditions intermediate to the two other stand-age classes, with little LWD and inputs of relatively easily decayed terrestrial debris (primarily red alder litter).

Differences between the three stand-age classes in certain characteristics and functions of LWD are accentuated in larger streams. Average piece size, pool frequency, and average pool area exhibit less difference in smaller streams than in larger systems. Differences by stand-age class in the amount of sediment accumulated by LWD or amount of fine organic matter associated with wood are less affected by stream size. In general, however, changes in LWD features and function after timber harvest of streamside vegetation tend to be most pronounced in larger streams.

Changes in LWD over Time

Models of changes in LWD abundance following removal of riparian trees have assumed a relatively slow decline caused by decomposition of residual in-channel wood. Swanson and Lienkaemper (1978) hypothesized that relatively little change in pre-harvest levels of LWD in Pacific Northwest streams would occur for 50 yr due to slow decomposition of pre-harvest LWD. A model by Grette (1985) proposed a linear decline in LWD amount with time, at a rate of slightly less than 1%·yr^{-1}. Input of LWD from the deciduous riparian vegetation resumes approximately 40 yr after harvest, but is insufficient to offset decomposition, leading to LWD amounts 50 yr after harvest of approximately 75% of the old-growth level. Murphy and Koski (1989) suggested a faster rate of decline for southeastern Alaska streams, with larger pieces of LWD being eliminated at the rate of 1–3%·yr^{-1}, depending on characteristics of the channel.

None of these models, however, accurately predicted the patterns of change in LWD abundance reported here. Using the regressions developed from our data for LWD frequency (Fig. 1) and average debris volume index (Fig. 2), we estimated wood volume in streams 5, 10, and 15 m wide for each stand-age class (Fig. 10A). The regressions in Fig. 5, 8, and 9 were used to calculate pool frequency, area of sediment accumulations, and volume of fine organic material (Fig. 10B, 10C, 10D). Three channel widths were examined, since mean LWD piece size is influenced by stream size (Bilby and Ward 1989) and, as a result, has an influence on input and elimination rate (Likens and Bilby 1982; Murphy and Koski 1989). We have assumed that our clear-cut sites were all 5 yr post-harvest and the second-growth sites were all 50 yr post-harvest.

Total volume of LWD per 100 m of channel decreased 22% from old-growth levels 5 yr after harvest and 35% after 50 yr in streams 5 m wide (Fig. 10A). The magnitude of decrease became progressively greater with increasing channel width, with a depression in LWD volume of 47 and 86% in channels 10 and 15 m wide, respectively, 5 yr after harvest. The very large drop in volume in the larger streams is an indication of the decrease in both piece frequency and piece size. LWD volume decreased 71 and 94% from old-growth levels in channels 10 and 15 m wide, respectively, 50 yr after logging. The rate of decrease in LWD abundance between our old-growth and second-growth sites is comparable with that reported in other studies (Grette 1985; Murphy and Koski 1989). However, our data showed that the majority of this decrease occurred within the first 5 yr after harvest.

Pool frequency in channels 5 m wide is only slightly greater at old-growth sites than at clear-cut and second-growth sites (Fig. 10B). However, in 10- and 15-m-wide streams, pool frequency decreased by more than 50% in the 5 yr after harvest and then changed relatively little over the next 45 yr. Estimated decreases in sediment stored by LWD over time were greater than 50% for all three sized streams, with nearly all the change occurring shortly after timber harvest (Fig. 10C).

Fine debris volume decreases at a much greater relative rate than LWD following removal of the streamside vegetation (Fig. 10D). Fine debris was reduced by about 90% within 5 yr of harvest, regardless of stream size. Little change in the amount of stored fine debris occurred between 5 and 50 yr post-harvest.

Management of Riparian Areas

Pacific Northwest states and provinces have recently instituted regulations or guidelines requiring retention of standing trees along stream channels during timber harvest to provide a source of future LWD. In Washington, from 50 to 200 trees

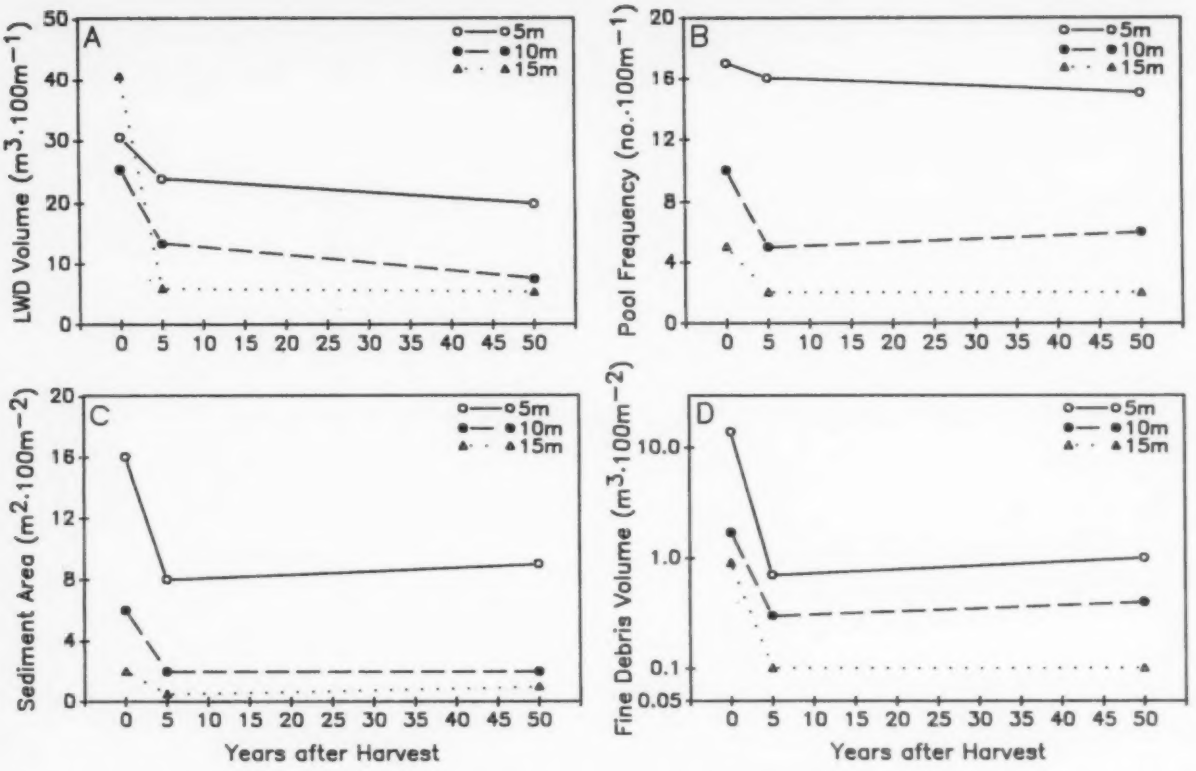

FIG. 10. Changes in LWD abundance and function with time after timber harvest for streams of three different widths. (A) Volume of LWD per length of channel; (B) pool frequency; (C) area of sediment accumulated by LWD; (D) volume of fine organic matter.

per 300 m of stream length must be retained after timber harvest, varying as a function of channel width (Bilby and Wasserman 1989). The width of the protected area also varies with stream size, ranging from 8 to 30 m on either side of the channel. Thus, the patterns of change in LWD abundance and function seen in this study resulted from timber harvest practices that are no longer in use. However, until the early 1980s, the trees along many streams were removed during timber harvest. The effect of this practice was the creation of riparian stands composed largely of red alder. Our data indicate that riparian zones with this type of vegetative composition (our second-growth sites) may not supply sufficient LWD, especially to larger streams. Also, the rapidly decomposing fine organic matter produced by deciduous vegetation is less effective at influencing channel structure than that from coniferous trees. Encouragement of conifer growth in riparian zones dominated by red alder may help alleviate some of these problems.

The vegetative and structural diversity of alder-dominated riparian stands may be increased by active management. Planting of conifer seedlings in riparian areas might be successful if the proper conditions for survival and growth can be created (Emmingham et al. 1989). Clearing small areas of riparian vegetation would be necessary in most cases to provide the conditions required by shade-intolerant conifer species, such as Douglas fir. Control of understory vegetation for several years could also be necessary. Release of suppressed conifers already present in the riparian area by removing the overstory is another possible option (Ferguson and Adams 1980).

The influence of fine organic debris on LWD function also suggests that vegetative characteristics of the riparian zone should be considered when selecting locations for stream habitat enhancement projects that include placement of wood. Our study indicates that LWD placement in streams would achieve improved results if conducted on a site receiving large inputs of fine coniferous debris.

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Appendix

TABLE A.1. Characteristics of the surveyed stream sections and the number of pieces of LWD measured at each site (o.g. = old-growth, c.c. = clear-cut, s.g. = second-growth).

Stream	Stand condition	Channel width (m)	Basin area (km^2)	Pieces measured (*N*)
Deschutes River Basin				
Hard Cr.	o.g.	5.6	1.7	60
Unnamed stream	o.g.	5.8	1.0	50
Mine Cr.	o.g.	7.5	2.7	50
Thorn Cr.	o.g.	7.6	3.6	52
West Fork Cr.	o.g.	9.0	8.7	51
Lewis Cr.	c.c.	3.8	3.0	50
Hard Cr.	c.c.	5.5	2.2	50
Upper Deschutes R.	c.c.	5.5	2.6	50
Little Deschutes R.	c.c.	5.6	3.9	50
Deschutes R.	c.c.	8.7	12.7	50
Thurston Cr.	s.g.	4.9	9.6	50
Mitchell Cr.	s.g.	8.3	21.9	50
North River Basin				
Fall R.	o.g.	12.4	30.4	50
Fall R.	c.c.	8.2	24.2	51
Unnamed stream	o.g.	3.6	2.1	50
Skookumchuck River Basin				
Unnamed stream	o.g.	4.2	0.8	50
Unnamed stream	o.g.	4.3	0.4	53
Unnamed stream	o.g.	5.4	2.3	50
Deer Cr.	o.g.	6.3	2.9	51
U. Skookumchuck R.	o.g.	7.1	1.7	50
L. Skookumchuck R.	o.g.	17.0	26.6	50
Unnamed stream	c.c.	4.6	1.3	50
Big Water Cr.	c.c.	6.3	5.2	60
Skookumchuck R.	c.c.	10.5	15.9	50
Upper Hanaford Cr.	s.g.	3.3	3.5	50
Laramie Cr.	s.g.	4.3	7.8	50
Three Deer Cr.	s.g.	4.4	4.5	51
Lower Hanaford cr.	s.g.	9.9	33.8	51
U. Skookumchuck R.	s.g.	11.0	60.6	50
L. Skookumchuck R.	s.g.	13.0	72.1	50

TABLE A.1. (*Continued*)

Stream	Stand condition	Channel width (m)	Basin area (km^2)	Pieces measured (*N*)
Abernathy Creek Basin				
Abernathy Cr.	s.g.	11.0	31.2	50
Newaukum River Basin				
Newaukum R.	o.g.	8.9	18.1	53
N.F. Newaukum R.	c.c.	7.0	19.0	50
Hemlock Hole Cr.	s.g.	5.6	9.1	50
N.F. Newaukum R.	s.g.	13.6	18.9	50
S.F. Newaukum R.	s.g.	13.8	60.6	50
Kalama River Basin				
Arnold Cr.	c.c.	3.7	2.6	50
Gobar Cr.	c.c.	12.3	54.3	48
Nisqually River Basin				
Hiawatha Cr.	c.c.	9.8	12.3	50
Little Nisqually R.	c.c.	13.7	21.9	50
Beaver Cr.	s.g.	7.6	29.0	50
Busy Wild Cr.	s.g.	12.3	41.9	50
Upper Mashel R.	s.g.	14.5	48.7	50
Middle Mashel R.	s.g.	19.3	96.3	47
Lower Mashel R.	s.g.	22.3	136.8	36
Coweeman River Basin				
Baird Cr.	s.g.	8.3	19.9	50
Lewis River Basin				
Upper Canyon Cr.	o.g.	10.1	12.7	50
Middle Canyon Cr.	o.g.	16.1	33.0	50
Fly Cr.	o.g.	18.9	50.3	46
Lower Canyon Cr.	o.g.	19.7	68.0	50
Canyon Cr.	c.c.	23.5	74.6	19

TABLE A.1. (*Concluded*)

Stream	Stand condition	Channel width (m)	Basin area (km^2)	Pieces measured (*N*)
Upper Chehalis River Basin				
Salmon Cr.	c.c.	9.9	55.4	50
Upper Chehalis R.	c.c.	12.5	29.6	51
Unnamed stream	s.g.	3.1	2.0	50
Capps Cr.	s.g.	3.3	2.6	50
Big Cr.	s.g.	5.6	9.3	50
S.F. Stillman Cr.	s.g.	9.5	23.1	50
S.F. Chehalis R.	s.g.	16.1	43.7	50
Willapa River Basin				
Trap Cr.	s.g.	9.9	23.3	50
Grays River Basin				
E.F. Grays R.	o.g.	11.7	7.5	49
N.F. Grays R.	o.g.	16.1	21.9	50
Toutle River Basin				
Eighteen Cr.	s.g.	5.2	5.9	50
Thirteen Cr.	s.g.	6.5	7.9	50
Devils Cr.	s.g.	7.1	16.1	50
Upper Hemlock Cr.	s.g.	7.1	13.5	50
Lower Hemlock Cr.	s.g.	8.4	30.6	50
Tilton River Basin				
M.F. Tilton R.	o.g.	5.9	1.3	50
Otter Cr.	o.g.	9.7	3.8	51
Wallanding Cr.	c.c.	14.2	20.5	50
N.F. Tilton R.	c.c.	23.1	83.7	30

Estimation of Temporal Acidification of Central Ontario Lakes

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The Wright–Henriksen model was used to estimate chemical changes in 255 central Ontario lakes attributable to strong acid loading. Background SO_4^{2-} in precipitation, 14.5 $\mu eq \cdot L^{-1}$, was estimated by analysis of "clean" events in contemporary data and used to determine background SO_4^{2-} in lakes, which averaged 26 $\mu eq \cdot L^{-1}$. Net (excess) SO_4^{2-} averaged approximately 100 $\mu eq \cdot L^{-1}$. An empirical function was used to calculate ANC_0 (at historical t_0) and ANC loss from net SO_4^{2-}. Then, pH_0 was estimated from ANC_0, obtained with empirical and theoretical relationships of contemporary pH_c and ANC_c. Almost all of ANC_0 of 125 $\mu eq \cdot L^{-1}$ on average was lost in one group of lakes near Sudbury. Associated mean pH decrease was 0.8–1.4 depending on the model used. Approximately 60–70% of ANC_0 of 110 $\mu eq \cdot L^{-1}$ was lost, with a pH decrease of 0.3–0.8, in lakes of two groups near Parry Sound. Only 20–30% of ANC_0 of 160 $\mu eq \cdot L^{-1}$ had been lost, with little pH change, in a group of lakes closer to Sault Ste. Marie. Such estimates are required for a rational interpretation of data on the distribution of fish species in Ontario lakes and estimation of losses of fish.

On a utilisé le modèle Wright–Henriksen pour estimer les changements chimiques, dans 255 lacs du centre de l'Ontario, attribuables à une forte charge acide. On a évalué la valeur de fond de SO_4^{2-} dans les précipitations à 14,5 $\mu éq \cdot L^{-1}$, en utilisant des cas de précipitations "propres" dans les données récentes, puis on a utilisé cette valeur pour déterminer la valeur de fond de SO_4^{2-} dans les lacs, laquelle serait en moyenne de 26 $\mu éq \cdot L^{-1}$. L'excès net de SO_4^{2-} était en moyenne de 100 $\mu éq \cdot L^{-1}$. On a utilisé une fonction empirique pour calculer la CNA_0 (au temps t_0) et la perte de CNA due au SO_4^{2-} net. On a ensuite calculé le pH_0 à partir de la CNA_0, obtenue par des relations empiriques et théoriques du pH_c et de la CNA_c à l'instant courant. Presque toute la CNA_0 de 125 $\mu éq \cdot L^{-1}$, en moyenne, était perdue dans un groupe de lacs de la région de Sudbury. Le pH moyen associé avait baissé de 0,8 à 1,4 selon le modèle utilisé. Dans les lacs de deux groupes de la région de Parry Sound, environ 60 à 70 % d'une CNA_0 de 110 $\mu éq \cdot L^{-1}$ étaient disparus et le pH avait baissé de 0,3 à 0,8. Pour un groupe de lacs voisins de Sault Ste. Marie, 20 à 30 % seulement de la CNA_0 de 160 $\mu éq \cdot L^{-1}$ avaient disparus, sans que cela modifie sensiblement le pH. Ces estimations sont nécessaires si l'on veut interpréter rationnellement les données sur la distribution des espèces de poissons dans les lacs de l'Ontario et se faire une idée des pertes de poisson.

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Differences in fish associations observed in synoptic surveys of Ontario lakes have been used to infer apparent losses of species richness due to acidification (Harvey and Lee 1982; Somers and Harvey 1984; Kelso et al. 1986; Matuszek and Beggs 1988). However, these differences might be attributable to naturally, spatially variable factors such as lake morphometry, hydrologic features, dissolved organics, alkalinity, or pH. Consequently, information on earlier conditions is needed, but often there are no historical data on lake chemistry and on fish communities, especially in smaller, headwater lakes which are more susceptible to acidification. Data on contemporary pH and alkalinity alone do not help us differentiate natural and anthropogenic factors, but interpretation of major ionic composition may permit estimation of historical lake chemistry. Then we may examine the extent that observed variability in fish species richness is related to chemical changes caused by atmospheric pollution.

Models that are useful in relating changes in pH and alkalinity to strong acid inputs and shifts in ionic composition have been available for at least a decade (Henriksen 1979; Thompson 1982; Wright 1983). They have evolved as knowledge of limnological processes improved (Glass et al. 1986; Rogalla et al. 1986; Minns et al. 1986; Marmorek et al. 1989; Schindler et al. 1989). It is surprising, therefore, that so little use has been made of these models in interpretation of data from surveys of fish species richness and fish associations, especially to attempt to untangle natural and anthropogenic factors that affect fish communities. Recently, Schindler et al. (1989) employed a model of this type to infer effects on biota in eastern U.S. lakes.

In the present study we used the Wright–Henriksen model (Wright 1983) to estimate the chemical changes in Ontario lakes attributable to strong acid loading and the original chemical state of these lakes. We surveyed lakes in four central Ontario watersheds which represented degrees of acidification from intensely acidified lakes in a highly sensitive and heavily acid-loaded region to lakes that have had much smaller changes in pH because of stronger buffering and lower acid loading. Unpublished data from several sources were made available to

us for this study. Databases from remote sites in the Precambrian Shield in Canada were useful in establishing a method to estimate background SO_4^{2-} in lakes. Also, relationships between acid-neutralizing capacity (ANC) and Ca + Mg in remote, unpolluted lakes provided the basis for a method to estimate changes in both ANC and Ca + Mg with acidification.

Methods

Features of the Lake Acidification Model

We used the Wright–Henriksen model (Wright 1983) to estimate the decline in ANC attributable to excess $H_2SO_4^{2-}$ inputs and estimated the historical pH_0 (at t_0) using both empirical and theoretical relationships between pH and ANC. The balanced cation–anion model is as follows:

$$(1)\quad Ca^{2+} + Mg^{2+} + Na^{+} + K^{+} + NH^{+}_4 + Al^{3+} + H^{+} = CO_3^{2-} + HCO_3^{-} + SO_4^{2-} + Cl^{-} + A^{-} + NO_3^{-}.$$

Initial assumptions are as follows.

(1) Ionic composition of Precambrian Shield lakes at t_0 generally is dominated by Ca^{2+}, Mg^{2+}, CO_3^{2-}, and HCO_3^{-} which determine pH_0. Organic anions (A^-) may influence pH when abundant relative to HCO_3^{-}.

(2) Acidification of central Ontario lakes is primarily attributable to H_2SO_4 inputs via precipitation (LaZerte and Dillon 1984). HNO_3 in precipitation has considerably less impact on lake pH because of uptake and storage of NO_3^{-} and NH_4^{+} in terrestrial systems (Nicolson 1988) and the opposite effect on pH of NO_3^{-} and NH_4^{+} (at low concentrations) in oxidation–reduction reactions.

(3) Extent of lake acidification is related to excess SO_4^{2-} loading over background (net SO_4^{2-} of Wright 1983). We opted for estimation of background SO_4^{2-} in each lake from SO_4^{2-} in precipitation at t_0 modified by evapotranspiration characteristics. Most of the SO_4^{2-} in Precambrian Shield lakes is from the atmosphere (Thompson and Hutton 1984; Neary and Dillon 1988). Hydrologic concentration factors (CFs) can be estimated from contemporary data on Cl^- in precipitation and lake water (Rogalla et al. 1986). However, it was necessary to check the assumption that background SO_4^{2-} originated from precipitation and to assess whether sulfur sinks and sources in watershed and lake might significantly affect lake water SO_4^{2-} concentration. Our method for calculating background SO_4^{2-} will be described subsequently.

(4) H^+ accompanying SO_4^{2-} will titrate ANC (mostly HCO_3^{-}) and/or exchange with Ca^{2+} and Mg^{2+} in watershed soils and lake sediments. The estimation of relative magnitude of each process will be examined later. We did not include Al–H^+ exchange in the model. Subregional estimates of change in alkalinity and pH were unaffected by including Al in the model used by Schindler et al. (1989) due to the small number of affected lakes. Al concentrations are low ($<5\ \mu eq \cdot L^{-1}$) in central Ontario lakes at pH 4.0–5.0 (J. Dillon, Ontario Ministry of Environment, P.O. Box 39, Dorset, Ont., P0A 1E9, pers. comm.).

(5) A^- was included in the model because there are many coloured as well as clearwater lakes that cannot be separated conveniently. That is, the lakes are a continuum of A^- concentrations, and even apparently clear lakes may have substantial A^- concentrations. We assumed that dissolved organic carbon (DOC) does not change substantially with acidification (Schindler et al. 1989), although A^- declines with increasing H^+ (Oliver et al. 1983).

(6) The assumption that Na^+, K^+, and Cl^- will not change from t_0 is reasonable, but data must be inspected carefully to detect road-salt pollution.

Estimation of Background SO_4^{2-}

Background SO_4^{2-} in precipitation may be estimated first from analysis of contemporary precipitation chemistry to define "clean" events (G. C. Pratt, Minnesota Pollution Control Agency, 1935 West County Rd. B-2, Roseville, MN 55113, unpubl. data and pers. comm.) or second by adoption of SO_4^{2-} values from remote areas. Precipitation data from the McKellar, Killarney, and Ramsay APIOS (Atmospheric Precipitation in Ontario Study) stations for 1981–83 (D. Green, Ontario Ministry of the Environment, 135 St. Clair Ave. West, Toronto, Ont., M4V 1P5, pers. comm.) were used in the Pratt model. Concentrations of SO_4^{2-} were increased (X1.2) to include estimated dryfall contributions (based on observations in central Ontario by Barrie and Sirois 1986; Sirois and Vet 1988; Semkin and Jeffries 1988). The Pratt model is a second-degree polynomial equation of pH versus SO_4^{2-}; minimum SO_4^{2-} at intermediate pH occurs in "clean" events. We employed the second method using data from the following remote areas: Nitchequon, Quebec, and Goose Bay, Labrador (CANSAP network of Environment Canada), Ear Falls, Ontario (APIOS network of Ontario Ministry of Environment), and the Saqvaqjuac study area, Northwest Territories (Welch and Legault 1986). We compared our results from the two methods, as well as estimates obtained with the Pratt model in other areas (G. C. Pratt, pers. comm.; Verry and Harris 1988). Our estimate obtained with the Pratt model was used in further calculations.

To examine our assumption that background SO_4^{2-} is derived from precipitation, we calculated lake water SO_4^{2-} from observed precipitation SO_4^{2-} and CFs for the Nitchequon, Goose Bay, Ear Falls, and Experimental Lakes Areaa (ELA) (near Kenora, Ontario) sites. Precipitation and runoff data were available for these sites (Water Survey of Canada, pers comm. and Newbury and Beatty 1980 for ELA). Predicted and observed lake water SO_4^{2-} were compared. The Saqvaqjuac lakes were not used because they occur on former marine sediments that are a source of lake water SO_4^{2-} (Welch and Legault 1986).

Background SO_4^{2-} in lakes could be obtained from SO_4^{2-} in precipitation at t_0 and a CF (neglecting, only for the moment, the possibility of watershed and lake sinks or sources of SO_4^{2-}). CFs (calculated as precipitation divided by runoff) obtained from watersheds in the Dorset study area (P. Dillon, pers. comm.) and Turkey Lakes study area (J. A. Nicolson, Great Lakes Forestry Centre, Sault Ste. Marie, Ont., P6A 5M7, pers. comm.) are quite variable. Therefore, we should have a CF for each lake. In the absence of hydrologic data, we examined the potential value of lake water Cl^- concentrations as weighting factors applied to accurately determined mean CFs from Dorset and Turkey Lake study areas. First, the data were screened carefully to eliminate lakes near and downstream from roads as potential sources of deicing salt. A dryfall correction (X1.2) was applied to precipitation Cl^-, reflecting observed relative contributions of Cl^- in dryfall and in "wet only" collectors (Cadle et al. 1986). We have assumed that hydrologic CFs have not changed substantially over time in these continuously forested watersheds, so that estimated CFs may be used in calculating background SO_4^{2-}.

Finally, SO_4^{2-} concentrations observed in lakes of the four study watersheds were compared with concentrations predicted from contemporary precipitation SO_4^{2-} and Cl-weighted CF to detect effects of sources or sinks for SO_4^{2-}. Organic soils may retain SO_4^{2-} (Bayley et al. 1986; Schindler 1986; Urban and Bayley 1986; Newton et al. 1987). Also, reduction of SO_4^{2-} within lakes consumes H^+ (Schindler and Turner 1982; Schiff and Anderson 1987), which may be substantial in lakes with long turnover times (Baker et al. 1986; Kelly et al. 1987).

Estimation of Loss of ANC

Mineral acidity associated with the excess SO_4^{2-} may take part in many reactions, but the two most important ones are in titrating ANC and in cation exchange with base cations, particularly Ca^{2+} and Mg^{2+}, in watershed soils (Dillon et al. 1980; Chistophersen and Wright 1981; Henriksen 1982; Thompson 1986; Wright et al. 1988) and in lakes (Oliver and Kelso 1982; Schiff and Anderson 1987). Therefore, two major changes in ionic composition at contemporary time t_c related to SO_4^{2-} are as follows, where Ca + Mg is the sum of Ca^{2+} and Mg^{2+} and net SO_4^{2-} is the increase from t_0 to t_c:

$$(2)\quad \mathrm{Ca} + \mathrm{Mg}_0 + F \cdot (\text{net } SO_4^{2-}) = \mathrm{Ca} + \mathrm{Mg}_c$$

$$(3)\quad \mathrm{ANC}_0 - (1 - F) \cdot \text{net } SO_4^{2-} = \mathrm{ANC}_c.$$

The F factor is usually in the range 0–0.4 in softwater lakes (Henriksen 1982; Wright et al. 1988), and it presumably approaches 1.0 as ANC_0 increases (Marmorek et al. 1989).

We obtained estimates of F for a series of nine intensively studied lakes in the Seguin and Shawanaga watersheds and these were correlated with estimates of ANC_0. The regression was used to estimate both ANC_0 and F for each lake in the database by means of iterative calculations and values of SO_4^{2-} and ANC_c (Equation 3).

Estimates of F for the nine lakes were obtained as follows: First we calculated ANC_0, Ca + Mg_0, and the values of ANC_0/Ca + Mg_0 from a series of assumed values of F through the range 0–1.0. The most likely value of F was that F giving a value of ANC_0/Ca + Mg_0 closest to observed ANC_c/Ca + Mg_c in remote lakes. In remote Precambrian Shield lakes, ANC may approach Ca + Mg concentration very closely where A^- is relatively low and less closely where A^- is higher relative to Ca + Mg (because ANC is partly titrated by organic acids). In the Department of Fisheries and Oceans Labrador lakes (Scrutton 1984), ANC/Ca + Mg was correlated with A^-. Where Ca + Mg was 50–150 $\mu eq \cdot L^{-1}$,

$$(4)\quad \mathrm{ANC/Ca + Mg} = 1.0 - 0.006\ \mathrm{A}^-$$

$$(n = 93,\ r = -0.724,\ P < 0.01).$$

Where Ca + Mg was <50 $\mu eq \cdot L^{-1}$:

$$(5)\quad \mathrm{ANC/Ca + Mg} = 0.86 - 0.007\ \mathrm{A}^-$$

$$(n = 25,\ r = -0.522,\ P < 0.01).$$

Over a range of 10–90 $\mu eq\ A^- \cdot L^{-1}$, ANC/Ca + Mg ranged from 0.46 to 0.94 (Equation 4) and from 0.23 to 0.79 (Equation 5). Therefore, in the selection of most likely values of ANC_0/Ca + Mg_0 and F, concentration of A^- was considered.

We repeated all calculations of ANC_0 based on an alternative assumption that all net SO_4^{2-} titrates ANC (that is, $F = 0$ always) and compared results from variable-F and zero-F variations within the model.

Estimation of Historical pH

Estimation of pH_0 at t_0 may be based on empirical relationships between pH_c and ANC_c over an appropriate range or it may be based on theoretical relationships among H^+, HCO_3^-, P_{CO_2}, A^-, and ANC. The regressions of pH_c on ANC_c for each watershed and season were used to estimate pH_0 (1) from ANC_0 (1) when $F = 0$ and to estimate pH_0 (2) from ANC_0 (2) when F was estimated and varied between 0 and 1.0. The sensitivity of the model to this variation in F when applied to these lakes will be examined. In addition, a theoretical model was used to estimate pH_0. In this case we used ANC_0 (2) obtained with the variable-F model to estimate pH_0 (3) at the same P_{CO_2} as occurred in contemporary sampling. P_{CO_2} at t_c was estimated from the relationship

$$(6)\quad K = H^+ \cdot HCO_3^-/P_{CO_2}$$

$$(\text{or } pP_{CO_2} = \mathrm{pH} + \mathrm{pHCO_3} - \mathrm{pK})$$

where pK = 7.8 and our measurement of ANC_c was substituted for HCO_3^-. We assumed that ANC and HCO_3^- are similarly related at t_0 and t_c. The lakes which had $ANC_c = 0$ were assigned the average value of P_{CO_2} from lakes where $ANC_c > 0$. Estimates of pH_0 (3) were obtained with the preceding equation and values for P_{CO_2} and ANC (2) for HCO_3^-.

We were not able to estimate pH_0 with the method of Schindler et al. (1989), which treats the effect of A^- on ANC explicitly, because it requires pH measurement in air-equilibrated samples.

Survey and Analytical Methods

Spring sampling was carried out in 1983 (April in the Seguin and Shawanaga watersheds and May in the Mahzenazing and Little Rapid watersheds) using a helicopter, while summer water sampling was done by helicopter or boat over the period June–October 1983. Smaller lakes were sampled at one station, while larger lakes (>100 ha) were sampled at two or three stations and measurements were averaged for further interpretation. Water was collected with a tube-integrated sampler or from 1 m deep with a VanDorn sampler and dispensed into cleaned 1-L nalgene bottles. Samples were refrigerated in darkness. The pH and ANC (by the Gran titration method) were measured in raw water using 0.02 N HCl and either a Corning or Orion 435 pH meter. Samples were filtered for other analyses (0.45-μm Millipore for DOC, Whatman 41 for major ions). Analytical chemistry was carried out by the Great Lakes Forest Research Centre, Environment Canada, at Sault Ste. Marie, Ontario, following published methods (Environment Canada 1979). Organic anions were calculated using the method of Oliver et al. (1983). The methyl – thymol blue (MTB) method (Environment Canada 1979) was in use for determination of SO_4^{2-} at that time; since then, interference by organics was reported (Thompson 1986; Kerekes et al. 1984). We corrected our data using the correlation ($r = 0.905$, $P < 0.01$) of the difference in SO_4^{2-} by ion-chromatography and MTB SO_4^{2-} with A^- concentration in more recent samples from a subset of our lakes. The MTB SO_4^{2-} concentrations (microequivalents per litre) were decreased by 0.16 × A^- concentration (microequivalents per litre).

Lake and watershed areas were measured from 1:50,000 topographic maps. Maximum depth was obtained by sounding line, and for the purpose of this work, mean depth was estimated from maximum depth using the equation $Z = 0.80 + 0.32\ Z(\mathrm{max})$ obtained from a subset of study lakes. The hydrol-

ogic turnover time of lakes was estimated from lake area and mean depth, together with watershed area and runoff data available from the Dorset study area (P. J. Dillon, unpubl. data) and Turkey Lakes study area (J. A. Nicolson, unpubl. data).

Description of Study Areas

All lakes 1.0 ha in area and larger in each of the four watersheds were sampled (Fig. 1). The 156 Seguin and Shawanaga lakes occur on bedrock mostly of clastic metasedimentary rocks, with areas of mafic anorthositic rocks in the headwaters of the Shawanaga and in the lower tributaries of the Seguin east–southeast of Parry Sound. Soils are particularly shallow, with much exposed bedrock in the lower Shawanaga, and bogs occur throughout the basins. The 52 Mahzenazing lakes occur partly in the quartzite hills of the Killarney Provincial Park region described earlier by Beamish and Harvey (1972) and Harvey and Lee (1982) and partly in formations similar to the Seguin and Shawanaga basins. The 47 Little Rapid lakes are in an area of older Precambrian, felsic igneous, and metamorphic rocks.

Lakes in the Mahzenazing watershed had the lowest mean pH, highest SO_4^{2-} concentrations, and little residual alkalinity (Table 1). The Seguin and Shawanaga lakes were slightly less acid than the Mahzenazing lakes in the spring and were about 0.5 pH unit higher in the summer sampling period. They had close to one half the SO_4^{2-} concentration and some residual alkalinity. In contrast, while the Little Rapid lakes had SO_4^{2-} concentrations similar to those in the Seguin–Shawanaga lakes, their acidity was 1/10 that of the other lakes. Organic anion concentrations were similar among lake groups. Although there is considerable variability in morphometric and hydrologic features, the lakes are of moderate area and shallow on average and they have short flushing times (Table 1).

At the time of the lake surveys, rates of wet deposition of SO_4^{2-} were 20–30 $kg \cdot ha^{-1} \cdot yr^{-1}$. Rates were highest in areas closer to Sudbury (Mahzenazing lakes), lowest to the northwest (Little Rapid lakes), and intermediate in the Seguin and Shawanaga watersheds.

Results

Estimates of Background SO_4^{2-} and Net SO_4^{2-}

Predicted lake water SO_4^{2-} concentrations obtained from SO_4^{2-} in precipitation and hydrologic data (Table 2) were generally similar to observed SO_4^{2-} concentrations within each set of lakes in remote areas and in the Dorset and Turkey Lakes study areas and in lakes of the present study where anthropogenic SO_4^{2-} loadings occur. The two factors, precipitation SO_4^{2-} which is higher closer to source regions and CF which decreases from west to east, have a dominant

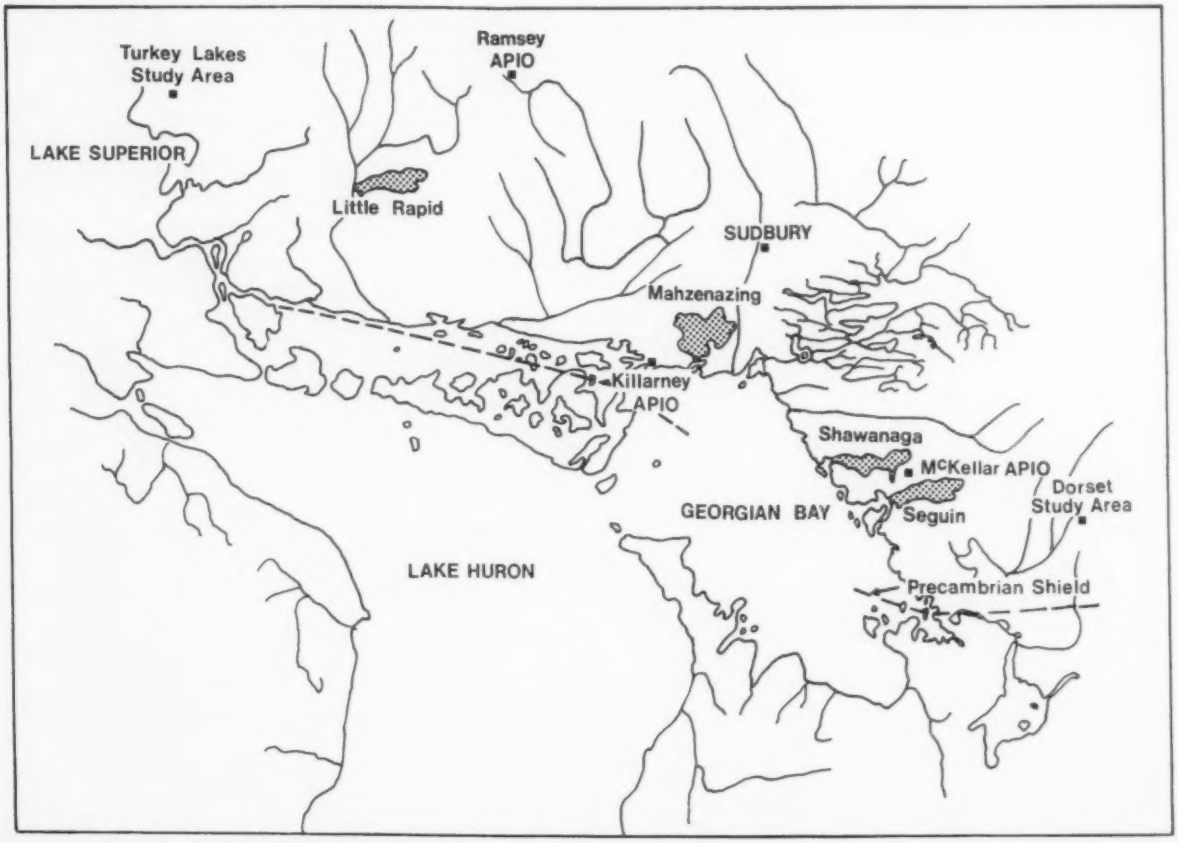

FIG. 1. Location of study watersheds and lake groups in central Ontario. Precipitation data were obtained from the three APIOS monitoring stations at Ramsey, Killarney, and McKellar. Unpublished hydrologic data were from the Turkey Lakes and Dorset study areas.

TABLE 1. Morphometric, hydrologic, and chemical characteristics of the four groups of lakes (standard deviations in parentheses).

Watershed	Number of lakes	Mean area (ha)	Mean depth (m)	Mean water residence time (yr)	Season	pH	μeq·L^{-1}							
							Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	ANC	Cl^{-}	A^{-}	SO_4^{2-}
Seguin	95	216	4.0	1.39	Spring	5.43	121.0	64.8	72.6	7.9	38.0	16.0	40.7	112.2
		(539)	(2.4)	(1.94)		(0.48)	(36.8)	(17.6)	(54.7)	(3.2)	(38.1)	(4.0)	(17.7)	(21.1)
					Summer	5.78	110.4	53.4	56.1	9.7	33.5	16.1	47.4	122.0
						(0.61)	(48.4)	(23.9)	(55.1)	(5.2)	(65.5)	(5.0)	(21.8)	(26.0)
Shawanaga	61	249	3.9	0.69	Spring	5.49	120.2	51.2	50.8	5.5	49.4	14.9	43.2	104.1
		(539)	(2.4)	(0.75)		(0.45)	(66.7)	(17.8)	(17.3)	(2.2)	(52.5)	(4.3)	(16.1)	(20.1)
					Summer	5.77	105.8	40.0	32.7	5.9	35.7	15.5	51.3	106.7
						(0.68)	(59.3)	(13.7)	(27.7)	(2.4)	(57.0)	(5.0)	(17.2)	(25.4)
Mahzenazing	52	41	2.9	0.90	Spring	5.30	110.0	61.1	30.2	10.9	7.5	10.1	39.9	182.7
		(76)	(1.8)	(1.40)		(0.55)	(38.4)	(19.7)	(11.2)	(2.9)	(25.5)	(3.1)	(12.3)	(43.2)
					Summer	5.32	115.0	65.2	34.8	9.5	1.3	10.9	41.9	205.0
						(0.68)	(37.0)	(21.0)	(9.1)	(3.9)	(30.2)	(4.6)	(15.4)	(45.8)
Little Rapid	47	309	3.0	0.82	Spring	6.63	184.1	88.2	39.2	7.4	91.7	12.6	59.8	122.3
		(687)	(1.9)	(0.96)		(0.36)	(46.9)	(38.6)	(6.0)	(3.1)	(42.6)	(3.3)	(38.8)	(29.4)
					Summer	6.71	162.3	72.4	63.3	6.4	148.9	16.1	53.5	127.3
						(0.45)	(62.3)	(31.0)	(61.5)	(2.0)	(70.7)	(4.6)	(22.7)	(40.8)

TABLE 2. Comparison of observed SO_4^{2-} in lakes with SO_4^{2-} predicted from SO_4^{2-} in precipitation. SO_4^{2-} in precipitation is the volume-weighted mean for 1981–83 from APIOS and CANSAP, from Linsey et al. (1987) for NW Ontario DFO, from Foster and Nicolson (1988) for the Turkey Lakes, and from Dillon et al. (1980) for the Dorset Lakes. Precipitation SO_4^{2-} was increased ×1.2 to include estimated dryfall. Hydrologic concentration factors are calculated from Water Survey of Canada (1.10), Newbury and Beatty (1980) (2.60), P. Dillon (pers. comm.) (1.87), and J. Nicolson (pers. comm.) (2.20). Data on observed SO_4^{2-} in lakes are from Clair et al. (1982) for Labrador DOE, Scrutton (1984) for Labrador DFO, Armstrong, and Schindler (1971) for NW Ontario DFO, B. Neary (pers. comm.) for NW Ontario OME, Jeffries et al. (1988) for the Turkey Lakes, and Harvey et al. (1981) for the Dorset Lakes.

Lake survey	Mean SO_4^{2-} in precipitation (μeq·L^{-1})	Hydrologic CF	Predicted SO_4^{2-} in lakes (μeq·L^{-1})	Observed mean SO_4^{2-} in lakes (μeq·L^{-1})
Labrador DOE	15.9 (CANSAP Nitchequon)	×1.10	17.5	20.1
Labrador DFO	15.9 (CANSAP Nitchequon)	×1.10	17.5	14.9
NW Ontario DFO	28.3 (ELA)	×2.60	73.6	63.0
NW Ontario OME	17.1 (APIOS Ear Falls)	×2.60	44.5	26.2
Turkey Lakes DOE	50	×2.20	110	116
Dorset Lakes DOE	69	×1.87	129	170
Seguin/Shawanaga DFO	77 (APIOS McKellar)	×1.87	145	113
Mahzenazing DFO	90 (APIOS Killarney)	×1.87	168	193
Little Rapid DOE	67 (APIOS Ramsay)	×1.87	125	125

influence on lake water SO_4^{2-}. There is evidence also of effects of watershed and/or lake sinks (northwestern Ontario Ministry of the Environment lakes, Seguin and Shawanaga lakes) and possibly sources as well (Mahzenazing lakes and Dorset lakes). These apparent sources may be attributable to washout of SO_4^{2-} from these systems, rather than natural sources, as precipitation inputs of SO_4^{2-} declined after 1980 (Kelso and Jeffries 1988). Lake water SO_4^{2-} concentrations in remote areas (Labrador and northwestern Ontario) probably approach background concentrations, although precipitation at ELA appears to include more anthropogenic SO_4^{2-} than precipitation at Ear Falls. However, background SO_4^{2-} likely was higher in northwestern Ontario than in northern Quebec and Labrador because of higher SO_4^{2-} in precipitation, as a result of mineral SO_4^{2-} in prairie dust, combined with higher CF (D. W. Schindler, University of Alberta, Edmonton, Alta., pers.

comm.). These results (Table 2) indicated that good estimates of background SO_4^{2-} in our lakes could be obtained from background SO_4^{2-} in precipitation and CFs. The data also suggested that watershed sinks, and perhaps sources, might affect present lake water SO_4^{2-}, and likely background SO_4^{2-} as well.

Background SO_4^{2-} concentrations in precipitation calculated by the Pratt model for eight stations (G. C. Pratt, pers. comm.; Verry and Harris 1988) were similar to observed SO_4^{2-} concentrations at four remote stations (Table 3), which supports our use of the Pratt model. For our study area, we used McKellar APIOS (Fig. 1) data in Pratt's model and obtained an estimate of background SO_4^{2-} in precipitation of 14.5 $\mu eq \cdot L^{-1}$.

Before we calculated a CF for each lake, using a Cl^--weighted mean CF (from hydrological data), Cl^- data were examined to detect sources and/or nonconservative behaviour. Predicted mean Cl^- concentrations in lakes of each watershed were obtained from precipitation Cl^- (a volume-weighted mean) and mean CF (Table 2) and these were compared with mean Cl^- observed in the lakes (Table 4). Predicted and observed mean concentrations of Cl^- were not significantly different. The variability of Cl^- in lakes was similar to that observed in hydrologic CFs calculated for watersheds in the Dorset study area. Coefficients of variation were 30 and 26%, respectively. The CF for each lake was calculated as CF × Cl^-/Cl^-. CF and Cl^- were determined for each watershed.

To detect possible sources and sinks for SO_4^{2-} in watersheds and lakes, observed lake water SO_4^{2-} in each lake was compared with predicted SO_4^{2-} (from observed SO_4^{2-} in preciptation in Table 2 and Cl^--weighted CF for each watershed and season). Retention of SO_4^{2-}, R, was calculated for each lake's watershed and season (Table 5).

Significant net removal of SO_4^{2-} (with mean R in Table 5 significantly different than zero) occurred in the Seguin watershed in spring and in the Shawanaga watershed in spring and summer. Significant removal did not occur in the Little Rapid watershed on average. Sources of SO_4^{2-} were apparent in the Mahzenazing watershed. In the Seguin and Shawanaga watersheds, 84% of lakes had net sinks in the spring which decreased to 68% in the summer, while in the Mahzenazing watershed, 70% had net sources in the spring and 78% had sources in the summer. In the Little Rapid lakes, net sinks and net sources occurred in nearly equal numbers and values of R were much less variable than in the other watersheds.

Values of R were highly significantly correlated with A^- in all watersheds and seasons except in the Mahzenazing watershed (Table 6). Presumably, A^- is proportional to the relative area of bogs in lake watersheds, where sinks occur. R was not inversely correlated with z/Tw (metres per year) from the model of Baker et al. (1986) which had agreed with observations in other studies (Kelly et al. 1987; Baker et al. 1986). However, a low percentage of our lakes (<10%) would be expected to have $R > 0.2$ according to their model. We have assumed that this reduction of SO_4^{2-} in natural sinks also occurred at t_0, with similar R values for each lake, and we included R in the determination of background SO_4^{2-} in lakes. However, net sources of SO_4^{2-} were apparent in some lakes, particularly in the majority of Mahzenazing lakes. This probably reflects washout of anthropogenic SO_4^{2-}, expected because SO_4^{2-} deposition declined after 1978 (Dillon et al. 1986). It was not appropriate to reflect these sources in estimates of background SO_4^{2-}.

In summary, background SO_4^{2-} in lakes was obtained as background SO_4^{2-} in precipitation × Cl-weighted CF × $(1 - R)$ where $R \geq 0$. Background SO_4^{2-} averaged 26.2 $\mu eq \cdot L^{-1}$ in the 255 study lakes. Values averaged 17% lower in the Seguin–Shawanaga lakes, relative to the Mahzenazing and Little Rapid lakes, primarily because of higher R in the Seguin and Shawanaga lake groups. Net SO_4^{2-}, the difference between contemporary and background levels, was significantly higher in the Mahzenazing lakes than in the other groups. The latter were not significantly different within seasons (Table 5).

Estimates of F

Loss of ANC was determined from residual ANC, estimates of net SO_4^{2-}, and F value for each lake within each seasonal data set (Equation 3). F was estimated as a function of ANC_0 in an iterative calculation. The regression was based on data from nine intensively studied lakes in the Seguin and Shawanaga watersheds representing varying degrees of acidification. Two examples of estimation of F (Fig. 2) illustrate how this

TABLE 3. Estimates of background SO_4^{2-} in precipitation. The first eight were estimated using the Pratt model. The last four were based on collection and analysis. Data sources: NADP, National Atmospheric Deposition Program (U.S.); MWPSG, Minnesota–Wisconsin Power Suppliers Group; MAP3S, Multistate Atmospheric Power Production Pollution Study; APIOS, Atmospheric Pollution in Ontario Study; CANSAP, Canadian Network for Sampling Precipitation.

Location	Model	Data source	Estimated SO_4^{2-} ($\mu eq \cdot L^{-1}$)
Fernberg Rd, MN	G. C. Pratt (unpubl. data)	NADP	17.9
		MWPSG	12.1
Monticello, MN	G. C. Pratt (unpubl. data)	NADP	20.2
Hubbard Brook, NH	G. C. Pratt (unpubl. data)	NADP	15.7
Huntingdon, NY	G. C. Pratt (unpubl. data)	NADP	14.2
Ithaca, NY	G. C. Pratt (unpubl. data)	MAP3S	8.5
Marcell, MN	Verry and Harris 1988	NADP	20.8
Aurora, NY	Verry and Harris 1988	NADP	19.6
Central Ontario	Pratt model: present study	APIOS	14.5
Nitchequon, Que.	Observed	CANSAP	15.9
Goose Bay, Labrador	Observed	CANSAP	15.2
Ear Falls, Ont	Observed	APIOS	17.1
Saqvaqjuac, N.W.T.	Observed	Welch and Legault 1986	17.6

TABLE 4. Comparison of predicted and observed Cl^- in lakes (confidence intervals of means ($P < 0.05$) in parentheses). Hydrologic CF used was 1.87 ($SE_z = 0.49$) for Seguin, Shawanaga, and Magzenazing and 2.2 ($SE_z = 0.50$) for the Little Rapid watershed (based on precipitation and runoff data from the Dorset and Turkey Lakes study areas, respectively). Precipitation means of Cl^- are volume-weighted means for 1981–83.

Precipitation station	Mean Cl^- in precipitation ($\mu eq \cdot L^{-1}$)	Prediced Cl^- in lakes ($\mu eq \cdot L^{-1}$)	Watershed	Season	Observed Cl^- in lakes ($\mu eq \cdot L^{-1}$)
APIOS McKellar	5.2	11.7 (5.2–18.2)	Seguin	Spring	16.0 (6.8–25.3)
				Summer	16.1 (4.2–27.9)
APIOS McKellar	5.2	11.7 (5.2–18.2)	Shawanaga	Spring	14.9 (6.0–24.0)
				Summer	15.5 (4.9–26.1)
APIOS Killarney	3.8	8.5 (3.7–13.3)	Mahzenazing	Spring	10.1 (3.7–16.5)
				Summer	10.9 (1.7–20.2)
APIOS Ramsay	2.5	6.9 (3.3–10.5)	Little Rapid	Spring	12.6 (6.1–19.1)
				Summer	16.1 (6.9–25.3)

TABLE 5. Ambient SO_4^{2-}, background SO_4^{2-}, and the difference between ambient and background termed net SO_4^{2-} (SE_z in parentheses). Concentrations of SO_4^{2-} predicted from precipitation SO_4^{2-} and hydrologic concentration are compared with ambient SO_4^{2-} and R is the estimate of SO_4^{2-} gained (sources) or lost (sinks), that is, $R = (SO_4^{2-}$ predicted $- SO_4^{2-}$ observed$)/SO_4^{2-}$ predicted.

Watershed	Season	n	Observed SO_4^{2-} ($\mu eq \cdot L^{-1}$)	Background SO_4^{2-} ($\mu eq \cdot L^{-1}$)	Net SO_4^{2-} ($\mu eq \cdot L^{-1}$)	Predicted SO_4^{2-} ($\mu eq \cdot L^{-1}$)	Mean R
Seguin	Spring	95	112.2 (2.2)	24.7 (0.5)	87.4 (1.7)	145.1 (3.7)	0.19 (0.02)
	Summer	100	122.0 (2.6)	25.2 (0.5)	97.4 (2.2)	145.1 (4.5)	0.07 (0.04)
Shawanaga	Spring	61	104.1 (2.6)	23.2 (0.6)	81.0 (2.0)	145.1 (5.3)	0.25 (0.03)
	Summer	53	106.7 (3.5)	22.8 (0.6)	83.9 (2.9)	145.1 (6.4)	0.20 (0.04)
Mahzenazing	Spring	52	182.7 (6.0)	29.9 (0.9)	152.8 (5.5)	168.5 (7.2)	−0.15 (0.05)
	Summer	41	205.0 (7.2)	29.8 (1.3)	175.1 (6.8)	168.5 (11.0)	−0.77 (0.47)
Little Rapid	Spring	47	122.3 (4.3)	28.2 (0.7)	94.0 (4.0)	125.5 (4.7)	−0.04 (0.05)
	Summer	43	127.3 (6.2)	29.1 (1.3)	98.2 (5.2)	125.5 (5.5)	−0.05 (0.05)

regression was obtained. A series of values of F from 0 to 1.0 were applied to net SO_4^{2-} to estimate ANC_0, $Ca + Mg_0$, and the quotient $ANC_0/Ca + Mg_0$ (Equations 2 and 3). The most reasonable and conservative estimate of F was the highest value that produced an expected value of ANC/Ca + Mg. This expected value of $ANC_0/Ca + Mg_0$ for each lake was determined from equations of $ANC_0/Ca + Mg_0$ versus A^- for the Labrador lakes within appropriate $Ca + Mg_0$ stratum. Estimated values of F for the nine intensively studied lakes varies from 0 to 1.0 (Fig. 3).

The relationship between F and ANC_0 was similar to that proposed by Marmorek et al. (1989); our data also suggested

TABLE 6. Correlation coefficients of R (SO_4^{2-} reduction or gain based on predicted SO_4^{2-}) in regression with z/Tw and A^-. In the model of Baker et al. (1986), z is mean depth (m) and Tw is residence time of water (yr). Significance levels: $*P < 0.05$ and $**P < 0.01$.

Watershed	Season	z/Tw	A^-
Seguin (n = 90)	Spring	0.175	0.346**
	Summer	0.209*	0.268**
Shawanaga (n = 61)	Spring	0.127	0.496**
	Summer	0.069	0.471**
Mahzenazing (n = 44)	Spring	0.004	0.156
	Summer	0.041	0.287
Little Rapid (n = 45)	Spring	0.055	0.475**
	Summer	0.223	0.303*

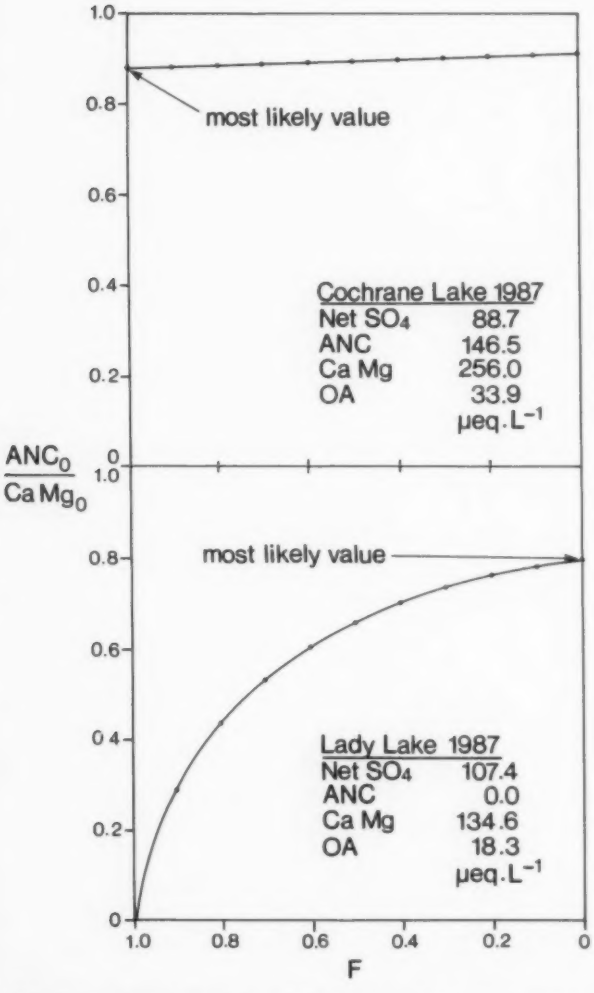

FIG. 2. Two examples of the calculation of $ANC_0/Ca + Mg_0$ at values of F between 0 and 1.0, one using Cochrane Lake data and the other using Lady Lake data. Selection of most likely values of $ANC_0/Ca + Mg_0$ to obtain appropriate F values is explained in the text.

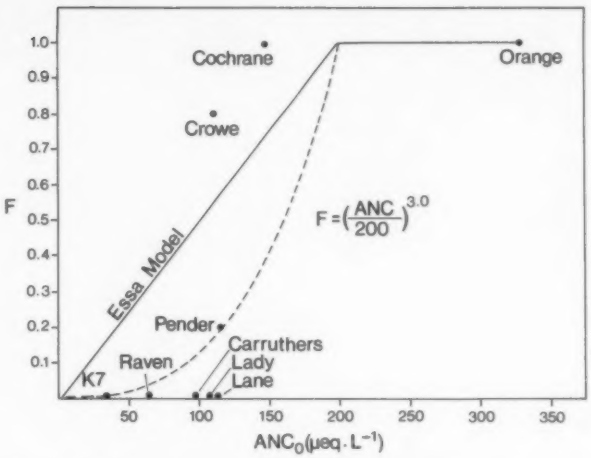

FIG. 3. Relationship between F and ANC_0. The regression was statistically significant (r = 0.746, $P < 0.05$). The line "ESSA model" is the relationship used by Marmorek et al. (1989).

an upper ANC_0 threshold of 200 $\mu eq \cdot L^{-1}$. The best statistical fit was to a nonlinear model, $F = \left(\frac{ANC_0}{200}\right)^{3.0}$, where F has an upper limit of 1.0. This relationship has lower values of F at given values of ANC_0 below 200 $\mu eq \cdot L^{-1}$ than the linear equation employed by Marmorek et al. (1989). Both models are crude approximations supported, unfortunately, more intuitively than experimentally at this stage in acid rain research.

Because we were interested in the sensitivity of predicted pH_0 to values of F selected, a model with $F = 0$ was used for comparison purposes. The averages of F in the variable-F model for lakes in the spring data set were 0.19 and 0.21 in the Seguin and Shawanaga systems, respectively, 0.24 in the Mahzenazing, and 0.41 in the Little Rapid. Summer values of F were within 10% of spring F values except in the Little Rapid which had a mean F of 0.66.

pH–ANC Relationships

Relationships between pH_c and ANC_c through an appropriate range of values were used to provide estimates of pH_0 from ANC_0. In this study, we have compared an empirical and a theoretical approach. Also, because two assumptions were made in evaluating F (constant = 0, and variable), four estimates of pH_0 were possible. However, data have been generated only for three of these, as described under Methods.

We included only lakes where $ANC_c > 0$ in regressions of pH_c on ANC_c because ANC_0 was probably positive in most, if not all, of these lakes. These empirical relationships (Fig. 4) differed among watersheds and seasons. The Seguin and Shawanaga lakes sampled shortly after loss of ice cover had lower pH_c relative to ANC_c than they had in summer. Hypolimnion samples also showed lower pH_c relative to ANC_c than epilimnion samples in the dimictic lakes in summer. Because A^- did not change much between periods or depths, we concluded that the difference was related to degree of supersaturation of CO_2.

We were unable to obtain more useful empirical relationships among pH and ANC when A^- was added in multiple regression analysis. A^- had no statistically significant effect on pH, except

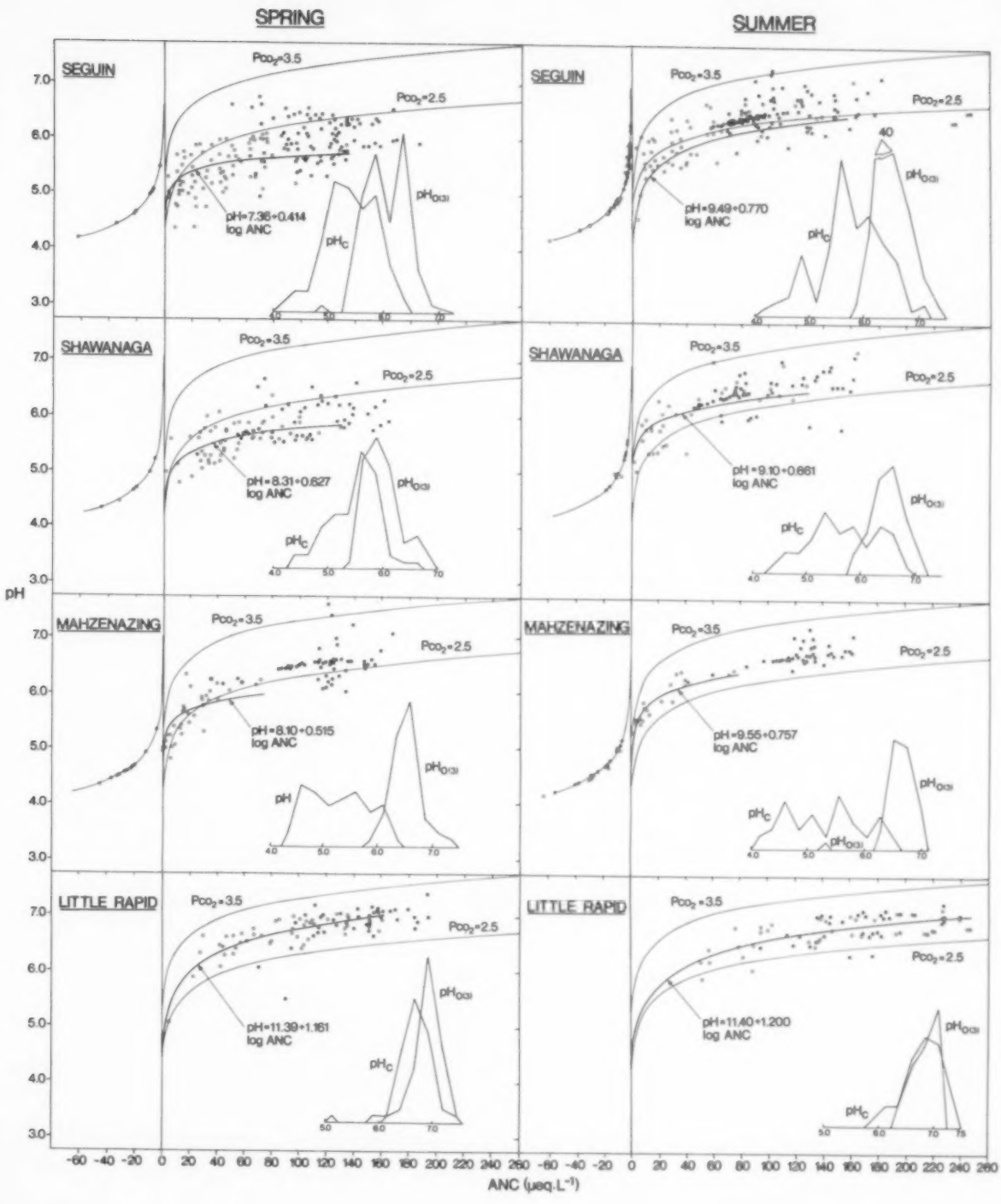

FIG. 4. Relationships of ANC_c and pH_c shown as solid circles; where ANC_c was negative, we have plotted H^+ concentrations. The heavy lines and equations were least-squares solutions of the equation $pH_c = a + b \log ANC_c$. Only observations where $ANC_c > 0$ were used. Values of pH_0 (3) predicted from values of ANC_0 (2) are shown as solid circles. Theoretical pH–ANC relationships at $pPCO_2 = 3.5$ (1 atm) and 2.5 are shown. The histograms show the frequency distribution of pH_c and pH_0 (3) values plotted at 0.25 pH unit intervals.

TABLE 7. Model output of predicted pH and ANC (SE_x in parentheses). ANC(1) was obtained with the assumption that $F = 0$, while ANC(2) was obtained with the variable-F model. With the use of empirical relationships, pH(1) was calculated from ANC(1) and pH(2) from ANC(2). Only ANC(2) was used in the theoretical relationship to calculate pH(3).

		Contemporary		$F = 0$		Variable F		
Watershed	Season	ANC ($\mu eq \cdot L^{-1}$)	pH	ANC(1) ($\mu eq \cdot L^{-1}$)	pH(1)	ANC(2) ($\mu eq \cdot L^{-1}$)	pH(2)	pH(3)
Seguin	Spring ($n = 95$)	38 (3.9)	5.43 (0.049)	126 (4.6)	5.74 (0.007)	108 (3.1)	5.71 (0.006)	5.99 (0.080)
	Summer ($n = 100$)	34 (6.6)	5.78 (0.061)	131 (7.1)	6.46 (0.015)	110 (4.9)	6.42 (0.013)	6.52 (0.029)
Shawanaga	Spring ($n = 61$)	49 (6.7)	5.49 (0.058)	130 (7.3)	5.85 (0.014)	113 (5.2)	5.82 (0.012)	5.95 (0.038)
	Summer ($n = 53$)	36 (7.8)	5.77 (0.094)	120 (9.5)	6.47 (0.020)	102 (6.2)	6.43 (0.016)	6.54 (0.064)
Mahzenazing	Spring ($n = 52$)	8 (3.5)	5.30 (0.077)	160 (7.1)	6.14 (0.010)	121 (3.2)	6.08 (0.007)	6.58 (0.050)
	Summer ($n = 41$)	1 (4.7)	5.31 (0.106)	177 (8.1)	6.70 (0.018)	126 (3.7)	6.59 (0.012)	6.74 (0.096)
Little Rapid	Spring ($n = 47$)	92 (6.2)	6.63 (0.053)	186 (8.7)	7.03 (0.024)	144 (4.2)	6.92 (0.016)	6.88 (0.033)
	Summer ($n = 43$)	149 (10.8)	6.71 (0.069)	247 (13.0)	7.04 (0.030)	179 (7.4)	6.89 (0.022)	6.86 (0.076)

in the Little Rapid lakes in spring only when the improvement over ANC alone was marginal. When the data were stratified into high, medium, and low A^-, with Seguin–Shawanaga data pooled and Mahzenazing – Little Rapid data pooled, the intercepts and slopes in the four pH–ANC equations were not significantly different.

Model Output

ANC_0

Means of ANC_0 (1) varied from 120 to 247 $\mu eq \cdot L^{-1}$ (Table 7); they were significantly higher in the Mahzenazing and Little Rapid than the Seguin and Shawanaga lakes. A significant seasonal difference occurred only in the Little Rapid lakes. Means of ANC_0 (2) ranged from 102 to 179 $\mu eq \cdot L^{-1}$. Little Rapid lakes had significantly higher ANC_0 (2) than the others, and again only the Little Rapid lakes had higher mean ANC_0 in the summer data set.

Means of ANC_0 (2) were always lower than means of ANC_0 (1) because $F > 0.0$ when ANC (2) was calculated. However, these means were not significantly different in Shawanaga and Seguin lakes because variable F had a low mean value in these watersheds. Therefore, the estimated decrease in ANC was similar in Seguin and Shawanaga lakes, approximately (80–95 $\mu eq \cdot L^{-1}$ using ANC_0 (1) and 65–75 $\mu eq \cdot L^{-1}$ using ANC_0 (2). In contrast, ANC_0 (2) was significantly lower than ANC_0 (1) in Mahzenazing and Little Rapid lakes. Consequently, the decline in ANC in the Little Rapid lakes was considerably less with ANC_0 (2), only 30–40 $\mu eq \cdot L^{-1}$ compared with about 90–100 $\mu eq \cdot L^{-1}$ based on ANC_0 (1). In the Mahzenazing lakes the mean decline was 150–175 $\mu eq \cdot L^{-1}$ based on ANC_0 (1) and 115–125 $\mu eq \cdot L^{-1}$ with ANC_0 (2). Whether these differences translate into a major or minor effect on pH at relatively high ANC_0 will be examined subsequently.

pH_0

Only small differences (<0.1 pH) occurred between estimates of pH_0 (1) and pH_0 (2) for each lake, the two empirical estimates using $F = 0$ and variable F, respectively (Table 7). In Seguin and Shawanaga lakes, this is attributable to similar values of ANC_0 (1) and ANC_0 (2). In the case of the Mahzenazing and Little Rapid lakes, with greater differences in ANC_0 (1) and ANC_0 (2), pH changed slowly at the high end of the empirical relationship between pH_0 and ANC_0.

Within seasons, mean pH_0 (2) in Seguin and Shawanaga lakes was similar, but these lakes had significantly lower mean pH_0 (2) than Mahzenazing and Little Rapid lakes (Table 7). Differences among the pH_c–ANC_c predicting equations for spring data (Fig. 3) are likely attributable mainly to higher P_{CO_2} in Seguin and Shawanaga lakes shortly after ice-out. Depressions in pH in winter and spring in northern Wisconsin lakes were attributable mainly to increases in P_{CO_2} (Kratz et al. 1987). Most of the difference in summer may be the result of approximately double the ANC_0 in Little Rapid lakes compared with Seguin and Shawanaga lakes. Differences due to P_{CO_2} should have been minimal at that time. The differences between pH_0 (2) in Mahzenazing and Little Rapid lakes were not as great, especially in summer when it appeared that differences in ANC could be the main factor (Table 7). These same observations apply to differences among values of pH_0 (1).

The means of pH_0 (3) were significantly higher than pH_0 (2) only in spring and excluding Little Rapid lakes. Estimates of pH_0 (3) were based on P_{CO_2} calculated from measured ANC_c and pH_c. Consequently, higher levels of P_{CO_2} (calculated with Equation 6) in the spring in Seguin and Shawanaga lakes yielded lower estimates of pH_0 (3) in these lakes than in Mahzenazing and Little Rapid lakes.

Changes in pH

Predicted average decreases in pH to contemporary levels based on pH_0 (1) and pH_0 (2) were not significantly different.

TABLE 8. Decrease in pH from pH_0 to pH_c obtained from two estimates of pH (SE_L in parentheses).

Watershed	Season	n	Decrease based on: pH(2)	pH(3)
Seguin	Spring	95	0.30 (0.045)	0.63 (0.050)
	Summer	100	0.64 (0.051)	0.75 (0.048)
Shawanaga	Spring	61	0.33 (0.049)	0.46 (0.038)
	Sumer	53	0.67 (0.082)	0.77 (0.074)
Mahzenazing	Spring	52	0.78 (0.072)	1.28 (0.87)
	Summer	41	1.28 (0.099)	1.42 (0.096)
Little Rapid	Spring	47	0.29 (0.040)	0.25 (0.026)
	Summer	43	0.18 (0.065)	0.15 (0.048)

Decreases based on pH_0 (3) were significantly greater than those based on pH_0 (2) only in the Seguin spring data and Mahzenazing spring data (Table 8). Long-term changes in spring were less than those in summer, except in the Little Rapid lakes. In summary, considering all methods equally useful at this point, long-term differences in pH in spring were 0.3–0.6 unit in the Seguin and Shawanaga lakes, 0.8–1.3 units in the Mahzenazing lakes, and <0.3 unit in the Little Rapid lakes. Using the summer data, we obtained estimates of change of 0.6–0.8 unit in the Seguin and Shawanaga lakes, 1.3–1.4 units in the Mahzenazing lakes, and < 0.2 unit in Little Rapid lakes. The lower values are from the empirical approach, while the higher estimates are from the theoretical model.

Multiple regression was employed to indicate variables most closely related to the decrease in pH. Four watersheds, two seasons, and three estimates of decrease in pH provided a total of 24 regressions in which the independent variables had been selected as follows: lake area (A_L), turnover time (Tw), lake order, A_W/A_L (where A_W is watershed area), A^-, and $Ca_0 + Mg_0$. In all but two cases, significant regressions ($P < 0.05$) were obtained with $R^2 > 0.25$ (n = 41–100). In 22 cases, Ca + Mg_0 was significantly, inversely correlated with pH decrease. In the summer data set, either lake order or Tw was also significantly and inversely related to pH change in all but one case (pH_0 (3) in the Little Rapid lakes) in which no variable was significant. Lake order and Tw were not cross-correlated in any lake group. Occasionally, A_W/A_L was significantly, positively correlated with pH decrease. In the spring data set, lake order was again important in the Seguin and Shawanaga lakes while A^- was sometimes significant.

Discussion

Methodology

The main problem in calculating the increase in lake SO_4^{2-} from anthropogenic sources is the estimation of background SO_4^{2-}. Rogalla et al. (1986) calculated background SO_4^{2-} of 20–80 $\mu eq \cdot L^{-1}$ in the upper Great Lakes region. They assumed that background precipitation SO_4^{2-} was between the global minimum (10 $\mu eq \cdot L^{-1}$) and estimates from Pratt's model (20 $\mu eq \cdot L^{-1}$), to which they applied a range in CFs to obtain lake SO_4^{2-}. Using their median CF of 3.3, their lake water SO_4^{2-} is about 50 $\mu eq \cdot L^{-1}$. Our estimates are lower than this mainly because the hydrologic CF is lower in central Ontario. Harvey et al. (1981) suggested that background SO_4^{2-} in the Great Lakes region of the Precambrian Shield averaged 60 $\mu eq \cdot L^{-1}$. Wright (1983) calculated background SO_4^{2-} of 26–41 $\mu eq \cdot L^{-1}$ in both remote and acidified areas in northeastern North America with higher levels, about 60 $\mu eq \cdot L^{-1}$, in the Great Lakes region. Our research suggests background SO_4^{2-} of 20–30 $\mu eq \cdot L^{-1}$ in central Ontario lakes, with higher concentrations to the west and lower concentrations to the east, related to continental patterns in hydrology (CF effect). The differences among estimates (30–40 $\mu eq \cdot L^{-1}$) would produce a large difference in net SO_4^{2-} in much of central Ontario, for example nearly a twofold difference in the Shawanaga lakes. Where SO_4^{2-} is especially high, as in the Mahzenazing lakes, differences in estimates of background SO_4^{2-} have relatively less effect on net SO_4^{2-}.

Our observations on the extent of SO_4^{2-} removed in sinks justified the use of a factor to reduce background SO_4^{2-} in lake water. Removal averaged almost 25% in Seguin and Shawanaga lakes. Contemporary sources of SO_4^{2-} were evident, especially in the Mahzenazing lakes. We attributed this to washout of largely anthropogenic SO_4^{2-} because of proximity to Sudbury and because inputs from the atmosphere had declined in central Ontario (Kelso and Jeffries 1988) and particularly from Sudbury smelters (Dillon et al. 1986). Former sinks may now be sources, and washout presently from these temporary sources would mask the former effects of sinks. Consequently, we may have overestimated background SO_4^{2-} in many lakes, especially in the Mahzenazing lakes.

The only satisfactory way to calculate F is from temporal trends in ionic composition in acidifying lakes, as a result of changing atmospheric or experimental loads. Wright et al. (1988) estimated F of 0.5 at the Sogndal, Norway, site. Unfortunatey, such observations are not numerous, and estimates will not be derived readily from theory or laboratory experiments because so many processes are occurring. Our estimates in the nine lakes averaged 0.3 but varied from 0 to 1.0. Modeled F values averaged about 0.2 in the Seguin, Shawanaga, and Mahzenazing lakes and 0.5 in the Little Rapid lakes. Henriksen (1982) reviewed extensive survey data and suggested that F probably had values between 0 and 0.4. Our estimates of F are relatively crude because the relationship of ANC to Ca + Mg at t_0 had to be generalized. The three models that might be initially considered for Precambrian Shield lakes in central Ontario are that $F = 0$, $F = 1.0$ (or close to these values), or F varies between 0 and 1.0 proportional to availability of base cations in sediments (cation exchange capacity and base saturation). Estimates of Ca + Mg_0 (or ANC_0) in lake water should be an adequate surrogate of cation availability. Observations on drastic peturbation of ANC/Ca + Mg in our lakes permit rejection of $F = 1.0$. The predicted values of pH_0 from the other two models of F were similar. In the case of lakes with higher ANC_0, pH_0 changed little over a wide range in ANC (see Fig. 4), so there was considerable latitude for error in estimation of F. At low ANC_0, predicted values of F were very low in the variable-F model, and

consequently, predicted values of ANC_0 from the two models were similar.

The most difficult problem we encountered was in estimating pH_0 from ANC_0 (and also from P_{CO_2} in the theoretical model). In using empirical models, we assumed only that the most appropriate pH_0 at a given ANC_0 is the observed pH_c at the same ANC. Only values of $ANC_c > 0$ were used in regressions for each watershed and season. These equations, which were used to estimate pH_0 (1) and pH_0 (2) with $F = 0$ and variable F, respectively, are subject to considerable background noise, well exemplified in this study. The Seguin and Shawanaga lakes were sampled shortly after ice-out and they apparently had higher P_{CO_2} than the other groups. Although a time-variable effect of P_{CO_2} is recognized, it is not dealt with explicitly in calculating pH_0 (1) and pH_0 (2). We calculated an alternative estimate, pH_0 (03), using the same value of P_{CO_2} as calculated from pH_c and ANC_c. We could have used other values of P_{CO_2} at t_0, thus standardizing results for our comparison of lake groups, which would have been more uniform consequently. For example, Herczeg and Hesslein (1984) suggested that pH could be calculated from dissolved inorganic carbon (DIC) and P_{CO_2} to avoid the effects of DOC on electrode pH, and pH could be normalized to ambient P_{CO_2} of the atmosphere. However, results with apparently high P_{CO_2} were informative because the significance of natural processes that alter pH is often overlooked (time of year, ice-cover, phytoplankton blooms). We appreciate that the differences in pH_0 among lake groups from spring data are attributable to survey methods and timing, yet they reflect natural pH cycles at t_0 that have ecological significance.

Finally, we believe that it would be unrealistic to select only uncoloured lakes to avoid analytical problems created by dissolved organics or to neglect seasonal effects of CO_2 supersaturation on pH. Therefore, the empirical relationships between pH and ANC may be most defensible on an ecological basis at the present time.

Lake Acidification

High net SO_4^{2-} in the Mahzenazing lakes indicated high acid loads that drastically reduced and often eliminated ANC. There was higher frequency of watershed sources of SO_4^{2-} than in the other lake groups, suggesting remobilization of $H_2SO_4^{2-}$ possibly from former sinks. There was no evidence that F was any lower on average than in the Seguin and Shawanaga lakes. In contrast, the Little Rapid lakes had lower net SO_4^{2-}, higher remaining ANC, and higher average values of F. Consequently, average pH in the Little Rapid lakes has declined by about 0.2–0.3 unit, while the decrease in pH was 0.8–1.4 units in the Mahzenazing lakes (based on pH_0 (2) and pH_0 (3)). The decline in pH in the Seguin and Shawanaga lakes was intermediate, 0.3–0.8 unit. Net SO_4^{2-} in the Seguin and Shawanaga lakes was similar to that in the Little Rapid lakes, but residual ANC was much greater in the latter. All of the lake groups had the same average A^- concentration, suggesting that differences in pH decrease among lake groups were not likely related to variability in the proportions of coloured lakes.

Schindler et al. (1989) estimated ANC and pH declines for nine U.S. subregions. Declines were highest in the northeast, about 50 $\mu eq\ ANC \cdot L^{-1}$ and 0.6–0.7 pH unit in the Adirondacks and Poconos–Catskills and lowest in the Midwest, $<10\ \mu eq \cdot L^{-1}$ and <0.2 pH unit in Minnesota, Wisconsin, and Michigan. The changes in the northeastern U.S. lakes are similar to those in the Seguin and Shawanaga lakes (Table 8). Changes in the Mahzenazing lakes were much greater (about $125\ \mu eq \cdot L^{-1}$ and 1.3 pH units based on pH_0 (2) and pH_0 (3) estimates for summer data) because of their proximity to the large SO_2 source at Sudbury.

Original chemical characteristics of lake groups were more similar than they are at present. Predicted average summer pH varied from 6.4 to 6.9 depending on ANC, which averaged $100–180\ \mu eq \cdot L^{-1}$. Differences in spring pH resulted from our sampling schedule which produced variability among pH–ANC regressions. Probably all lakes had lower pH (5.7–6.0) in early spring under ice or shortly after ice-out. Peak pH probably occurred during phytoplankton blooms in surface waters. The annual minimum pH probably occurred in hypolimnia of dimictic lakes prior to fall mixing. Hypolimnetic waters had highest P_{CO_2} in our surveys (authors' unpublished data).

Strong inverse correlation of pH change with pH_c and pH_0 indicated that the lakes with lowest pH_0 (and pH_c) changed most because they had least buffering. The net result, therefore, is an increase in the variance in pH_c over that in pH_0 in each group of lakes where substantial change in pH occurred. This is apparent in the comparisons of pH_c and pH_0 (3) in Fig. 4, especially in the case of the Mahzenazing lakes.

Four potentially important factors which reduced the effect of acid loads to these lakes are chemical reduction of SO_4^{2-} in watershed sinks, exchange of H^+ with base cations in watershed soils or lake sediments, reduction of SO_4^{2-} in the lakes, and high ANC_0 in lakewaters. Reduction of SO_4^{2-} appeared to be more important in the watershed than in lakes, based on finding similar concentrations of SO_4^{2-} in lakes and in 12 monitored streams that drained watersheds without lakes (authors' unpublished data). This conclusion was supported by significant correlations between SO_4^{2-} reduction and A^- concentration (indicative of relative abundance of bog). Also, SO_4^{2-} reduction was not inversely correlated with z/Tw, probably because a small minority of our lakes had appropriate morphometry and hydrology for substantial SO_4^{2-} reduction according to the model of Baker et al. (1986). Reduction of SO_4^{2-} was close to 25% in Seguin and Shawanaga lakes; this was likely a minimal estimate because we measured the net effect of sinks and sources, with the latter becoming increasingly important since atmospheric loads decreased. Cation exchange was equally important in the Seguin, Shawanaga, and Mahzenazing lakes with F averaging 0.2–0.25. Cation exchange was apparently more important than watershed sinks in the Little Rapid lakes because F averaged 0.54. High ANC_0 buffered acid load to the greatest extent in the Little Rapid lakes and to the least extent, on average, in the Seguin and Shawanaga lakes. Mahzenazing lakes had intermediate ANC_0, but this was insufficient for maintenance of ANC in many lakes because acid load was nearly twice that in other lake groups. Morphometric and hydrologic factors which often accounted for significant amounts of the variance in pH decline were lake order, Tw, and A_W/A_L. Lakes with low order and Tw and with high A_W/A_L had the greatest changes in pH. Therefore, the most sensitive lakes on a hydrologic and morphologic basis are the rapidly flushing headwater lakes. Often, many headwater lakes are also lower in ANC and may have lower reductions in acid input due to watershed sinks and cation exchange than downstream lakes. This is because a wider range in characteristics occurs in headwater lakes compared with "averaged" conditions downstream as flows converge.

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Factors Related to the Biomass and Production of Fish Communities in Small, Oligotrophic Lakes Vulnerable to Acidification

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Kelso, J. R. M., and M. G. Johnson. 1991. Factors related to the biomass and production of fish communities in small, oligotrophic lakes vulnerable to acidification. Can. J. Fish. Aquat. Sci. 48: 2523–2532.

We estimated biomass and production of the fish community in 19 small (<50 ha) lakes from four watersheds in central Ontario. Lake pH ranged from 4.8 to 7.1. We found 19 fish species in these lakes; yellow perch (*Perca flavescens*), pumpkinseed (*Lepomis gibbosus*), white sucker (*Catostomus commersoni*), and largemouth bass (*Micropterus salmoides*) were the most common. On average, there were 4.5 species per lake. Neither fish community biomass nor production was significantly different among the communities identified by cluster analysis, and the number of fish species was not lower at lower pH. More than 75% of each lake's total biomass was confined to less than three fish species. Whole-lake fish biomass was related to the total number of species in the lakes and their average age. Fish community production was related to fish biomass, averge fish size, and acid neutralizing capacity (ANC) with an almost equal influence provided by each factor. At lower ANC and pH, fish were usually smaller in weight and often had lower population growth rates. In these lakes where the influence of lake size and trophic status was minimized, fish community biomass and production were only secondarily related to lake pH or ANC.

On a estimé la biomasse et la production de poisson dans 19 petits lacs (<50 ha) de quatre bassins du centre de l'Ontario. Le pH de ces lacs était compris entre 4,8 et 7,1. On a trouvé 19 espèces de poissons dans ces lacs; les plus communs étant la perchaude, (*Perca flavescens*), le crapet-soleil (*Lepomis gibbosus*), le meunier noir (*Catostomus commersoni*) et l'achigan à grande bouche (*Micropterus salmoides*). En moyenne, il y avait 4,5 espèces par lac. A l'analyse par clusters, ni la biomasse de poisson ni la production ne différaient beaucoup selon les communautés identifiées, et le nombre d'espèces ne diminuait avec le pH. Plus de 75 % de la biomasse de chaque lac étaient constituées par moins de trois espèces. La biomasse totale de poisson était liée au nombre total d'espèces et à leur âge moyen. La production des communautés de poissons était reliée à leur biomasse, à la taille moyenne des individus et à la capacité de neutralisation des acides (CNA), et on peut dire que chaque facteur avait à peu près la même influence. Lorsque la CNA et le pH étaient plus bas, les poissons étaient généralement plus petits et avaient des taux de croissance inférieurs. Dans les lacs où l'effet de la taille du lac et de son niveau trophique était minimisé, la biomasse et la production des communautés de poissons n'étaient reliées au pH et la CNA que de façon secondaire.

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The generally small, >55% of Canadian lakes are less than 10 ha (Fisheries and Environment Canada 1978), and oligotrophic (Laycock 1987) lakes of Canada are susceptible to a variety of ecosystem perturbations. It is unreasonable to measure the consequences directly from either regionally operating stresses (e.g. acidic atmospheric deposition, climatic warming) in individual lakes or from exploitation of inland fisheries affecting vast areas; therefore, freshwater scientists are increasingly using models to assess biological effects in broad geographic regions (e.g. Minns et al. 1986, 1990; Schindler et al. 1989; Minns 1990; DeAngelis and Cushman 1990). The regional models in popular use are restricted to assessing changes in the number of aquatic species, the distribution patterns of a species, or the yield of fish. Unfortunately, empirical models are often not calibrated for the small lakes to which they are applied and results may thus be imprecise. Further, as discussed by Ryder (1982) regarding the morphoedaphic index, factors relating to yield may be confounded, as relationships have not been tested in lakes where effects of some variables have been constrained in order to evaluate the importance of others.

In addition to the need for adequately testing fishery models for small lakes and identifying lake properties related to model outputs, Downing et al. (1990) noted that probably the most important deficiency of lake fishery production models was that few actually predict either biomass or rates of production. Instead, available fishery models predict "yield" or "catch" whereas the management of fisheries is based on biomass (see Ricker 1975). The use of yield or catch as a convenient surrogate assumes that sustainable fish yield is correlated with production. As Downing et al. (1990) found, fish community production data were available only for 20 lakes in the world and results came from diverse environments using differing methods. Consequently, their analysis could only partly address

the chemical, physical, and biological factors influencing fish community production and could be inappropriate for small, temperate, oligotrophic Canadian lakes.

Also, although we suspect that acid neutralizing capacity (ANC) and pH might be related to fish yield, catch, biomass, or production, there have been limited attempts at separating the effects of pH (or ANC) from other factors. Catch (per unit of effort, CPUE) is usually negatively correlated with pH (Beggs et al. 1985; Beggs and Gunn 1986) and lake morphometric characteristics have been identified as covariates (Kelso and Gunn 1984; Kelso et al. 1986). However, fish growth or condition (where condition (K) = weight/length^3) has been both higher and lower at low pH's (Ryan and Harvey 1980; Harvey 1982; Rosseland 1986; Frenette et al. 1986; Kelso et al. 1986, 1990). Consequently, our understanding of the relationship between lake fishery production and pH or ANC is, at best, incomplete.

As a result, we estimated fish community biomass and production in 19 small (from 5 to 38 ha) lakes on the Canadian Shield receiving roughly similar annual atmospheric deposition (>10 but <20 mmol wet SO_4^{2-}/m^2; Barrie and Hales 1984) but ranging in pH from 4.6 to 7.2 after fall overturn (Johnson et al. 1991). We assumed that the effects of lake size would be minimized and that natural trophic state would be generally similar. Our hypothesis was that fish community production would be less at low pH because fewer species may be present, biomass might be lower, and growth may be less.

Physical/Chemical Characteristics of the Study Lakes

Our 19 lakes (Table 1) are located in four watersheds: Seguin (Cochrane, Carruthers, Lane, and Pender), Shawanaga (Raven, Crow, K7, Orange, Lady), Mahzenazing (Billie, Grey, Turbid, Black, and Gayney), and Little Rapid (G18, G36, P10, G22, and Aa5), proceeding from south to north in north-central Ontario on the Canadian Shield (see Johnson et al. (1991) for further details of the lakes in these watersheds). Each watershed contains from 100 (Seguin) to 232 (Mahzenazing) lakes which are, with the exception of one lake in the Mahzenazing watershed, all <1000 ha (Cox 1978). Approximately 85% of the lakes in the watersheds are <100 ha.

Lakes (19) for which we collected fish population data are small (from 5 to 38 ha, mean = 14.5) and generally shallow (mean depth from 1.3 to 5.3 m, mean = 2.9), but they have a large range (25–820 ha, mean = 228) in drainage basin size (A_W). Water renewal times (calculated by dividing the lake volume by the product of A_W times the average annual precipitation runoff coefficient (from Fisheries and Environment Canada 1978)) were short (0.09 – 3 yr, mean = 0.8). Only five of the 19 lakes had water renewal times >1 yr and these lakes were in either the Seguin or Shawanaga watersheds.

While the variability in physical features of these lakes is constrained, there are differences in pH, ANC, Ca^{2+}, SO_4^{2-}, dissolved organic carbon (DOC), and to a lesser extent total phosphorus (Table 2). To compare pH differences among lakes, we used pH measured after fall overturn but before ice had formed. Five lakes had pH < 5, four lakes had a pH between 5 and 6, and 10 lakes had pH > 6. All lakes were coloured to some extent, as indicated by a continuum of DOC concentrations. Three lakes (G36, P10, and Raven), however, were clearer, and three lakes (G22, Black, and K7) were highly coloured.

Experimental Methods

We selected lakes that were accessible by road or over a short (<0.5 km) portage. Lakes in the Little Rapid and Mahzenazing watersheds had comparatively difficult access and most were fished infrequently by anglers, if at all. Approximately half the lakes in the other two watersheds were also difficult to access and were probably not fished intensively by anglers. We did not select lakes with specific fish species assemblages although considerable variety existed within these watersheds (M. G. Johnson, J. R. M. Kelso, and C. K. Minns, unpubl. data).

To capture fish, we used trap nets, gill nets, angler minnow traps, and seine nets. On the first two visits to each lake, we

TABLE 1. Morphometric and physical characteristics for 19 lakes from four watersheds in north-central Ontario.

Lake	Lake area (A_0, ha)	Maximum depth (m)	Mean depth (m)	Drainage area (A_w, ha)	Lake vol. (10^5 m^3)	Lake perimeter (km)	Longest length (km)	A_0/A_w	Turnover time (yr)
G18	14.0	4.5	1.9	71	2.65	2.2	0.9	0.2	0.6
G36	9.0	4.0	1.7	46	1.53	1.4	0.8	0.2	0.6
P10	13.0	3.0	1.3	788	1.70	2.6	1.0	0.0	0.0
G22	5.0	4.0	1.7	55	.85	0.7	0.3	0.1	0.3
Aa5	13.0	5.5	2.3	140	2.95	2.2	0.9	0.1	0.4
K21 Billie	20.0	5.3	2.2	141	4.40	3.6	0.7	0.1	0.5
K22 Grey	38.0	12.0	4.6	408	17.52	4.6	1.8	0.1	0.7
K25 Turbid	17.0	4.9	2.1	819	3.48	3.3	1.4	0.0	0.1
K18 Black	9.0	6.2	2.5	280	2.27	1.6	0.7	0.0	0.1
P1 Gainey	19.0	10.0	3.9	236	7.43	3.2	1.5	0.1	0.5
14NO Carruthers	10.0	5.5	2.7	75	2.75	1.6	0.6	0.1	0.8
01 Lady	5.8	7.2	4.6	25	2.67	1.3	0.6	0.2	2.1
33 Lane	18.5	6.0	3.1	90	5.76	2.4	0.8	0.2	1.3
K7	7.5	9.0	3.8	632	2.86	1.8	0.6	0.0	0.1
Al Orange	9.8	5.3	2.1	35	2.09	1.2	0.5	0.3	1.2
20 Cochrane	18.9	5.2	3.2	158	6.07	2.1	0.8	0.1	0.8
04 Pender	22.7	16.8	5.3	82	12.07	4.4	1.1	0.3	3.0
K12 Raven	13.6	8.5	3.2	207	4.37	2.2	0.8	0.1	0.4
C1 Crow	11.5	3.5	2.6	48	3.05	2.7	1.2	0.2	1.3

TABLE 2. Selected lake chemical properties for 19 lakes from four watersheds in north-central Ontario. Concentrations are in mg/L except where noted.

Lake	pH	ANC (μeq/L)	Sulphate	Calcium	Magnesium	Sodium	Potassium	Total N (μg/L)	Total P (μg/L)
G18	6.6	64.0	5.3	2.6	0.7	0.6	0.2	0.3	5.7
G36	7.1	221.0	5.6	4.4	1.3	0.9	0.4	0.4	11.0
P10	7.2	300.0	7.8	2.3	0.7	3.9	0.2	0.2	5.0
G22	6.3	79.0	8.2	4.0	1.0	0.8	0.2	0.3	17.0
Aa5	6.9	117.0	5.2	3.4	0.7	0.7	0.3	0.2	6.8
K21	4.8	−14.2	9.4	1.8	0.7	0.6	0.3	0.4	14.0
K22	4.9	−10.8	10.2	1.9	0.7	0.7	0.4	0.4	12.0
K25	4.8	−12.7	11.0	2.2	0.8	0.8	0.3	0.3	8.0
K18	5.5	36.0	7.8	1.8	0.6	0.8	0.8	0.8	13.1
P1	6.1	56.0	8.5	2.6	1.1	1.4	0.4	0.3	7.9
14NO	5.8	27.0	9.3	2.0	0.6	4.0	0.2	0.4	7.9
O1	5.2	2.0	13.0	1.6	0.5	0.5	0.4	0.3	4.9
33	6.0	20.0	13.6	2.2	0.6	0.6	0.3	0.3	6.9
K7	4.6	0.0	7.3	0.9	0.4	0.4	0.2	0.6	14.9
A1	7.0	280.0	13.6	8.0	1.2	3.0	0.5	0.5	16.1
20	6.6	137.0	12.1	3.2	1.0	1.0	0.5	0.4	11.1
04	6.2	52.0	10.7	2.2	0.7	0.5	0.3	0.4	5.9
K12	4.9	0.0	9.0	1.0	0.3	0.4	0.2	0.4	7.9
C1	6.1	85.0	9.7	3.0	0.6	0.6	0.4	0.6	18.2

fished at least three of the four gear types to determine fish species present and the most appropriate gear for the species present. Thereafter, we always used trap nets and angler minnow traps to capture fish for marking and usually used all four fishing gears if the recapture period was separated from the marking period.

Traps nets were of two different constructions (leads 15.3 or 30.6 m long, 5-cm stretched measure mesh, cribs constructed of either 2.5- or 5-cm mesh) and were set perpendicular to shore in all 19 lakes. Nets were moved to new locations usually on a daily basis and were removed from the lakes on weekends. Because our goal was to capture and mark as many fish as possible within a short period (2 wk was tentatively scheduled for each lake), we used from two to four trap nets per lake. Gill nets (seven panels of 3.8-, 5.1-, 6.4-, 7.6-, 8.9-, 10.2-, and 12.7-cm stretched measure multifilament mesh, each panel 1.8 × 9 m) were also used in all lakes to supplement trap net samples when catches were low, to provide a diversity of gear types and to estimate abundance when the removal method was used. When fish were to be marked or released using gill nets, nets were continuously patrolled and fish were removed within 1–5 min, usually <2 min, to enhance survival after capture and marking. "Small" fish were captured by angler minnow trap nets (also called baitfish traps) and seine nets. Mesh sizes of both the minnow traps and seine nets were 6 mm. Minnow traps were moved daily and seine hauls were made at all suitable sites in each lake. We fished from 12 to 20 minnow traps daily and made up to 20 seine net hauls in each lake. Further gear descriptions and details of procedures can be found in Dodge et al. (1982).

Captured fish were held in onboard containers, narcotized (Alka Seltzer tablets) when needed to ease handling, measured, and weighed. Also, three or more scales and one to two fin rays were removed for age determinations. If >20 fish of one species were captured in a day, the catch was subjectively subsampled. Fish were marked with individually numbered Floy spaghetti tags if total length was >12 cm, or distinctively fin clipped (<12 cm) to identify release sites. Once marked, fish were kept in aerated lake water for a recovery period of 3–8 min and only healthy individuals were released.

We estimated the abundance of fish present using either the Petersen (Chapman modification), Schumacher, or Leslie method (Ricker 1975). Our strategy for abundance estimation was to mark as large a portion of the population as possible in the fall (late September and October) and recapture animals in the spring (May and early June), thus allowing adequate time for mixing of marked and unmarked animals during a period when growth was minimal. Where access made frequent visits difficult, or when sample size was large and recaptures frequent, we used the data collected in the fall to estimate population size by the Schumacher method. Whether the Petersen or Schumacher method was used, we calculated abundance at the end of each day's fishing effort and stopped sampling only when the abundance estimate and its confidence limits changed little, i.e. N changed <10%, on three consecutive days. In two lakes (Lady and K7) where fish were not abundant and recaptures were less than four, introducing the potential for statistical bias (see Robson and Regier 1964; Ricker 1975), our only option to estimate abundance was to intensify the gill net effort and estimate population size by the removal method (Leslie method). Leslie estimates of abundance and confidence limits were calculated according to Ricker (1975). Our methods constrain all estimates of abundance to the fall.

In our view, the "best" estimates of abundance were by the Petersen method, where time allowed mixing, followed by estimates made using the Schumacher and Leslie methods. In any case, we attempted to reduce possible error by (1) moving nets on a daily basis, (2) using a fall marking and spring recapture period, when appropriate, to allow "mixing" of marked fish in the population, (3) minimizing recruitment effects by selection of a time when growth was reduced, (4) minimizing stress from capture and handling, (5) using different fishing gears for recapture, (6) adjusting effort in each lake such that the product of the number marked and the number in the capture sample was large, greater than three times the estimated population size, thereby reducing statistical bias in Petersen estimates (Robson and Regier 1964), and (7) matching the "best" method of estimating abundance to the number of fish captures and recaptures and the ease of capture for the fish species present.

We estimated abundance by both the Petersen and Schumacher methods for five populations of brook trout (*Salvelinus fontinalis*), six populations of white sucker (*Catostomus commersoni*), and two populations of northern redbelly dace (*Phoxinus eos*) in seven lakes in the Little Rapid and Mahzenazing watersheds. Regression analysis of the Petersen and Schumacher estimates of abundance indicated that the slope, 1.02, was significant ($T = 7.81$, $P < 0.05$) and the proportion of the variance attributed to the relationship was high ($r^2 = 0.85$, $N = 13$).

Numerical abundance of each fish species (N_i) and the average weight of the catch (w_i) were used to estimate biomass ($B_i = N_i \cdot w_i$) of that species (fraction vulnerable to the capture gear). Individuals from each population were aged using scales or fin ray sections. From the ages and mean weights, we calculated an instantaneous population growth rate (G_x; Ricker 1975; Bagenal and Tesch 1978). We determined the biomass of the fish community (B_c) by summing the biomasses of each species ($B_c = \Sigma B_i$) in the lake. Annual production of the fish community in each lake (P_c) was estimated by $P_c = \Sigma B_i \cdot G_x$.

We used a single measure of fish biomass (B_i) to approximate production rather than estimate an average biomass (Ricker 1975) because recruitment to our capture gear was reasonably complete in the fall and because we were interested in comparing lakes. This approach conforms with Chapman (1978).

To determine factors relating to whole-lake fish biomass (B_c) and production (P_c), we first classified the fish community by clustering (Gauch 1984). We used Jaccard's dichotomy coefficient for the matrix of fish presence–absence data and used the complete linkage agglomeration (Legendre and Legendre 1983) to sort the fish communities in the 19 lakes. This method was used to maximize the difference among lakes because our lake selection process would, if anything, contribute to a similarity in community structure. Results of the clustering procedure were later used to determine if B_c or P_c was different among the fish communities.

To objectively reduce the number of lake descriptors (from a total of 18) and to determine the contribution of lake properties to the variation among the lakes (Green 1979), we performed principal components analysis. We then used the factor scores from the principal components analysis in a multiple linear regression model to determine if the principal components were related to B_c or P_c. If a significant relationship ($P < 0.05$) was found with any of the components' scores, we then used the data for the variable(s) loaded heavily upon that component in a regression analysis.

The clustering procedure, principal components analysis, and statistical tests were conducted with SYSTAT (Wilkinson 1988).

Results

Fish Community

In total, we found 19 fish species (Table 3). Yellow perch (*Perca flavescens*), white sucker, pumpkinseed (*Lepomis gibbosus*), and largemouth bass (*Micropterus salmoides*) were the most common species and occurred in 12, 11, 10, and 9 lakes, respectively. On average, there were 4.5 species per lake (range from one to eight species). Because the lakes in the four watersheds contained fish communities with from one to eight species, we tested whether the number of fish species in a lake was related to lake characteristics. No significant relationship using a linear multiple regression model was found between the total number of fish species or the number of species for which we estimated abundance and any physical or chemical property, including pH and ANC.

Species composition of fish communities differed among the watersheds. Brook trout, brook stickleback (*Culaea inconstans*), and blacknose shiner (*Notropis heterolepis*) were found only in lakes of the Little Rapid watershed. Smallmouth bass (*Micropterus dolomieui*) was found only in the Seguin and Shawanaga watersheds. Only white sucker occurred in lakes of all four watersheds. Lakes in the Little Rapid watershed (G18, G36, P10, G22, and Aa5) generally had a different fish community from those of the remaining three watersheds. Brook trout, white sucker, and cyprinids were common in the Little Rapid watershed, and two to five species occurred in each lake. Two lakes in the Mahzanazing watershed contained only pumpkinseed, and one lake in the Seguin watershed had only yellow perch. In general, lakes from the Mahzanazing, Seguin, and Shawanaga watersheds often contained centrarchids (four species) and/or yellow perch. These three watersheds also had few cyprinids.

In the cluster analysis of lakes by the presence or absence of fish species, a reasonably high degree of similarity existed among lakes (Fig. 1) even using a clustering procedure designed to maximize differences; however, lakes tended to group within watersheds. Lakes in the Little Rapid watershed (P10, Aa5, G36, G22, and G18) had brook trout, white sucker, and a variety of minnows and clustered together. Four lakes in the Seguin and Shawanaga watersheds (Lady, Pender, Lane, and Orange) containing smallmouth bass, largemouth bass, and yellow perch also grouped together. Billy and Grey lakes contained only pumpkinseed. The remaining large group of eight lakes were from the Mahzenazing (three lakes), Seguin (two lakes), and Shawanaga watersheds (three lakes) and contained a diverse community including centrarchids, white sucker, and brown bullhead (*Ictalurus nebulosus*).

Fish Abundance and Growth

We were able to estimate abundance of 54 fish populations occurring in the 19 lakes.[1] We captured some of, but were unable to estimate the abundance of, 29 fish populations because there were too few individuals in those populations. Where population estimates were made but too few (<30) fish were aged or measured (only four of 54 fish populations), we used the population growth rate (G_x) from fish in the nearest lake with adequate information.

Our procedures for estimating fish abundance underestimated population size. Rare species were not included in estimates of B_c and P_c. Also, age 0 fish may not have been adequately sampled by our four gear types. Further, the removal method for estimating fish abundance (Leslie method used when catches were low in K7 and Lady Lakes) tends to underestimate population size in lakes (see Kelso and Shuter 1990). On the other hand, we have confidence in our use of the data because (1) methods were consistent among lakes, (2) precautions were taken to reduce error and/or bias in the method of estimating abundance, (3) the method of estimating abundance was adapted to the patterns of fish capture in each lake, and (4) the Schumacher and Petersen methods closely agreed when both

[1]Complete set of data is available at a nominal charge from the repository of unpublished data, CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2, Canada.

TABLE 3. Total biomass (kg/ha) of each fish species[a] in 19 central Ontario lakes. Zero biomass indicates that the species was present but too rare to estimate abundance.

Lake	WS	BT	PS	YP	LB	SB	RB	LC	GS	ST	CC	RD	PD	CS	FD	BB	NP	CM	BS
G18	42.7							0	0										
G36	180.5	185.1								0	0	0							
P10	415.6	32.3								0		3.3	1.3	6.0					
G22	14.4	6.7																	
Aa5	219.2	41.0								0	0.2	4.4	0		0				0
K21			78.9																
K22			253.5																
K25			250.5	73.0												0			
K18			141.6	1090.0	0				0							195.0	0	0	
P1	39.5		135.5	53.1	86.8		1.8										6 3		
I4N0 Ca	231.8		502.9	344.4	36.5				0		0			0		95.7			
01				21.0															
33				67.3	41.4	138.3													0
K7			0	2.0	0	0			0							3.6			
A1	0			0		266.4										25.9			
20	280.8		0	37.5	167.0		109.9			0						30.6			
04	81.4			34.9	231.0	94.8													
K12			89.2	40.7												6.9			
C1	95.5		34.2	0	0		93.5									0			

[a]WS, white sucker (*Catostomus commersoni*); BT, brook trout (*Salvelinus fontinalis*); PS, pumpkinseed (*Lepomis gibbosus*); YP, yellow perch (*Perca flavescens*); LB, largemouth bass (*Micropterus salmoides*); SB, smallmouth bass (*Micropterus dolomieui*); RB, rock bass (*Ambloplites rupestris*); LC, lake chub (*Couesius plumbeus*); GS, golden shiner (*Notemigonus crysoleucas*); ST, brook stickleback (*Culaea inconstans*); CC, creek chub (*Semotilus atromaculatus*); RD, northern redbelly dace (*Phoxinus eos*); PD, pearl dace (*Semotilus margarita*); CS, common shiner (*Notropis cornutus*); FD, finescale dace (*Phoxinus neogaeus*); BB, brown bullhead (*Ictalurus nebulosus*); NP, northern pike (*Esox lucius*); CM, central mudminnow (*Umbra limi*); BS, blacknose shiner (*Notropis heterolepis*).

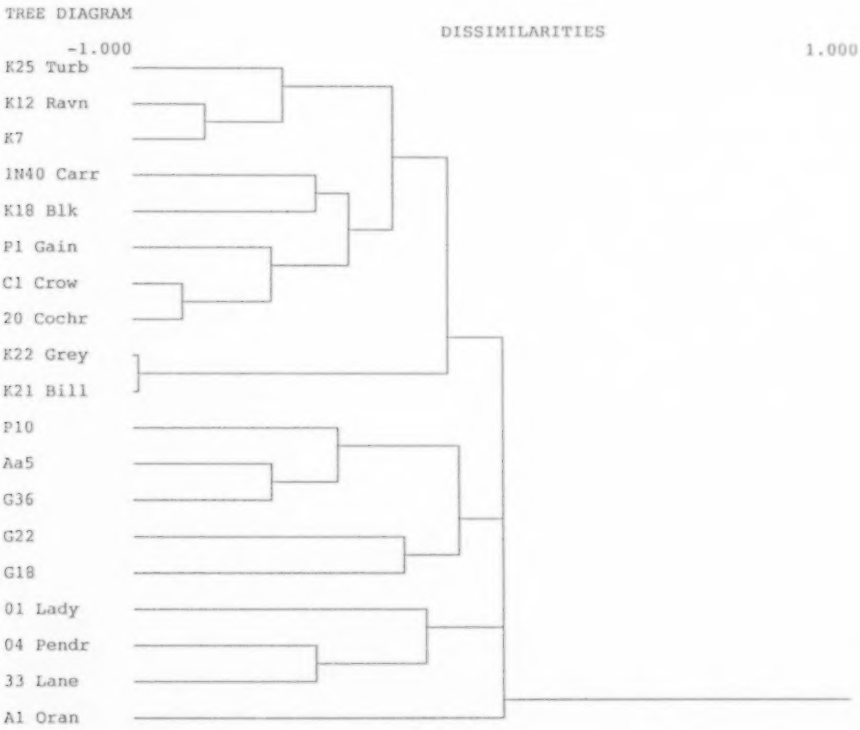

FIG. 1. Cluster diagram for all species in 19 lakes from four watersheds in north-central Ontario. Lakes grouping to the left have the highest degree of similarity.

were used to estimate abundance for 13 populations occurring in seven lakes.

In general, there were more fish in lakes in the Mahzenazing watershed (five lakes, average total N = 12 230) followed by lakes in the Seguin (four lakes, average total N = 9070), Little Rapid (five lakes, averge total N = 4080), and Shawanaga watersheds (five lakes, average total N = 1730). Total abundance of fish was not correlated with lake size.

The highest estimates of abundance were for yellow perch where Black lake was estimated to contain >20 000 fish. Pumpkinseed were also abundant, as four lakes contained >5000 fish. Carruthers (Seguin) and Black (Mahzenazing watershed) lakes were estimated to contain >20 000 fish. Eleven lakes were estimated to contain fewer than 5000 fish, while five lakes had 5000 to 10 000 and one lake had 15 000 to 20 000 fish.

The average weight and population growth rates for each fish species differed among the lakes in which they occurred. Unfortunately, few fish species were ubiquitous, and an evaluation of lake factors that were related to fish size or growth was restricted to white sucker (10 lakes), yellow perch (eight lakes), and pumpkinseed (seven lakes). Only the total number of fish species in the lake and pH or ANC were significantly related to average w_i or G_x of the three species. Results were inconsistent among the species in part because our sample size was small. G_x was significantly less at lower pH for white sucker, and average weights of pumpkinseed were less at lower pH. However, the average weight of the fish community (Table 4) was significantly ($P < 0.05$) related to both lake pH (averge weight = −239 + 56.9 pH, r^2 = 0.73, F = 19.5) and ANC (average weight = 62 + 0.45 ANC, r^2 = 0.65, F = 12.5). While our results indicate that fish size and possibly population growth rates of some species may be influenced by pH, we feel that our data are not conclusive.

Whole-Lake Fish Biomass and Production in Relation to Lake Characteristics

To avoid the problem of intercorrelation and to reduce the number of variables, we performed principal components analysis on the lake physical and chemical data. The first five principal components (Table 5) explained 82% of the variation in our 19-lake data set. Morphometric characteristics (lake area, depth, and lake size descriptors) and indicators of buffer status (lake pH, ANC, and Ca^{2+}) all loaded heavily on the first principal component. Lake characteristics relating to water renewal capability (watershed area, lake size, and turnover time) loaded heavily on the second principal component. Nutrients, lake length, and several major cations and anions loaded heavily on the final three principal components.

The standardized factor scores (Wilkinson 1988) were regressed against community fish biomass and production estimates (expressed per unit area) for each lake. When factor scores from the principal components analysis were regressed against biomass (B_c) in a stepwise fashion, there was no significant relationship with any of the five factors. However, when two lakes (Black and Carruthers) that had the highest biomass of fish (Table 4) were removed from the data set, scores from the first principal component (morphometry and buffer status) were significantly related to biomass. We had neither biological nor statistical basis for removing these two lakes from our data set; however, when biomass and ANC were plotted (Fig. 2), Black and Carruthers lakes did not appear to conform to the general trend. When we regressed the nine lake characteristics that loaded heavily (Table 4) on the first principal component against B_c in a multiple linear regression, only ANC proved to be significant (B_c/ha = 8.62 + 0.10 ANC, N = 17, r^2 = 0.80; $P < 0.001$). It appears that B_c was related only to ANC and, even so, there were exceptional lakes with high B_c.

To determine which lake characteristics were related to fish production, we regressed factor scores against whole-lake production (P_c). Three factors, first, second, and fourth components (Table 4), were significantly ($P < 0.10$) related to P_c in the stepwise regression ($P < 0.10$). However, when we used data for the variables that loaded heavily on each principal component, only ANC was significantly related to production in the

TABLE 4. Total biomass (B), production (P), average age f all species in the population (avg. age), average weight (av. wt.), total number of species in the population (tot. sp.), and the number of species for which we were able to make B and P estimates (sp. est.) for 19 lakes from four watersheds in north-central Ontario.

Lake	Total B_c (kg)	Total P_c (kg yr)	B_c/ha	$P_c \cdot ha^{-1} \cdot yr^{-1}$	Avg. age (yr)	Avg. wt. (g)	Tot. sp.	Sp. est.
G18	42.7	36.8	3.1	2.6	2.3	88.0	3	1
G36	365.5	317.1	40.6	35.2	2.4	244.0	5	2
P10	458.4	300.7	35.3	23.1	2.5	72.4	6	5
G22	21.2	10.5	4.2	2.1	2.4	120.3	2	2
Aa5	264.8	72.9	20.4	5.6	2.8	78.8	8	4
K21	78.9	53.8	4.0	2.7	4.0	15.6	1	1
K22	253.5	127.8	6.7	3.4	3.1	31.2	1	1
K25	323.5	60.2	19.0	3.5	3.3	20.9	3	2
K18	1424.6	192.5	158.3	21.4	4.6	55.0	7	3
P1	382.9	118.7	20.2	6.3	5.0	58.5	6	6
14NO	1211.4	288.4	119.9	6.8	4.7	80.0	8	5
01	21.0	4.7	3.6	0.8	4.0	64.2	1	1
33	246.9	101.8	13.4	5.5	3.6	130.9	5	3
K7	5.6	0.7	0.7	3.7	2.7	49.0	5	2
A1	292.3	163.3	29.8	0.1	16.7	221.4	4	2
20	625.9	232.4	33.1	12.3	3.5	162.5	7	5
04	442.1	425.8	19.5	18.8	3.6	179.9	4	4
K12	136.8	42.6	10.1	3.2	4.0	28.4	3	3
C1	223.2	78.8	19.4	5.3	2.7	129.5	6	3

TABLE 5. Component loadings from principal components analysis for physical/chemical properties of 19 Ontario lakes.

	1	2	3	4	5
Component loadings					
LAREA	−0.764	−0.199	−0.219	0.457	0.068
MAXZ	−0.799	0.251	0.158	0.015	0.002
MEANZ	−0.807	0.272	0.292	−0.155	−0.115
AWHA	−0.197	−0.625	−0.383	0.352	−0.306
VOLM3	−0.852	0.293	−0.019	0.344	0.044
LAKEPER	−0.821	0.098	−0.242	0.339	0.059
LLENGTH	−0.661	0.017	−0.322	0.528	0.095
AoAw	0.045	0.868	0.222	−0.271	0.105
TURNT	−0.368	0.766	0.234	−0.356	−0.105
PH	0.602	0.547	−0.364	0.152	0.145
ALKALINITY	0.672	0.398	−0.345	0.315	−0.136
SULPHATE	−0.232	0.453	0.274	−0.050	−0.630
CALCIUM	0.631	0.596	0.031	0.345	0.018
MAGNESIUM	0.453	0.493	−0.146	0.530	0.192
SODIUM	0.415	0.137	−0.394	0.146	−0.629
POTASSIUM	0.105	0.148	0.633	0.503	−0.107
TOTALN	0.119	−0.098	0.862	0.222	−0.114
TOTALP	0.316	−0.099	0.628	0.399	0.117
DOC	0.196	−0.438	0.635	0.349	−0.005
Variance explained by components	5.690	3.516	3.019	2.199	1.111
Percent of total variance explained	29.948	18.503	15.889	11.572	5.847

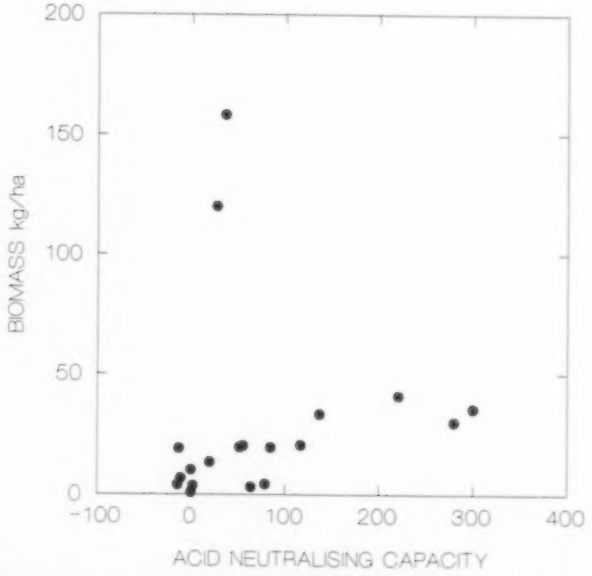

FIG. 2. Relationship between biomass (B_c) and ANC for fish from 19 lakes from four watersheds in north-central Ontario.

multiple regression. For all lakes, the regression between production and ANC was significant (P_c/ha = 4.01 + 0.07 ANC, $r^2 = 0.70$, $P < 0.001$). When Black and Carruthers lakes were removed from the data set, the relationship with ANC was improved only slightly and the slope did not change:

TABLE 6. Percent of total fish biomass by top rank species (1 to 5) and total number of species (richness) in 19 Ontario lakes.

	Rank					
	1	2	3	4	5	Richness
G18	99.99	0.01				3
G36	50.62	49.37	0.71	0.28		5
P10	90.65	7.04	1.31			6
G22	68.21	31.79			2	
A5	82.78	15.48	1.66	0.07		8
K21	100					1
K22	100					1
K25	77.44	22.56				3
K18	76.51	9.94	13.55			7
P1	35.38	13.86	17.30	0.48		6
14NO	41.51	28.43	19.14	7.90		8
01	100					1
33	55.99	27.26	16.75			5
K7	64.90	35.05	0.02	0.02	0.02	5
A1	91.13	8.87				4
20	44.87	26.69	17.56	4.89		7
04	52.24	21.44	18.42			4
K12	65.18	29.77	5.05			4
C1	42.78	41.90	15.32			7

N	Intercept	Slope	r^2	P
		Biomass, B_c		
19	No significant relationship			
17	8.62	0.10	0.81	<0.001
		Production, P_c		
19	4.01	0.07	0.70	<0.001
17	2.72	0.07	0.77	<0.001

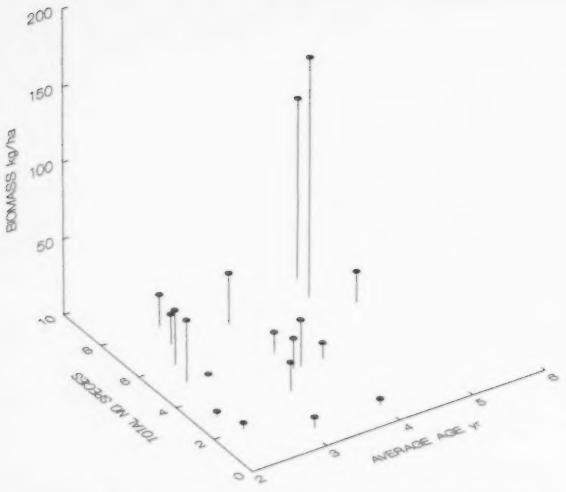

FIG. 3. Relationships among biomass (B_c), total number of species in the lakes and average age of the fish population for 19 lakes from four watersheds in north central Ontario.

Constraints on Biomass and Production Imposed by the Fish Community

While lake ANC was significantly related to whole-lake fish production (and perhaps biomass), these also could be influenced by the number of fish species present, the fish species in the community, and fish growth rates. Because the number of species within a lake ranged from one to eight, we first looked at the contribution by individual fish species to total fish community biomass (B_c, Table 6). In total, 19 species were found in these lakes (Tables 3 and 6) but >75% of total fish biomass was contributed by one species (nine lakes), two species (eight lakes), or three species (two lakes). The fish species that contributed most of the whole-lake biomass were, in order of frequency, white sucker, pumpkinseed, yellow perch, brook trout, largemouth bass, smallmouth bass, and brown bullhead where they occurred. Evidently, the majority of fish biomass within a lake was contributed by only a few species in the lake and, within the community structure in our lakes, was not dependent on the particular species in the assemblage.

To determine whether the association of fish species present was related to fish community biomass, we first tested whether there was a significant difference in biomass of the four communities identified by clustering (Fig. 1). Analysis of variance ($F = 0.56$, not significant $P > 0.05$) failed to detect a significant difference in biomass among the different communities.

Next, we examined the influence of the total number of species, the number of species for which we estimated biomass and production, the average age of the population(s), and their average weight on biomass (B_c) and production (P_c). The multiple regression for biomass indicated that average age and total number of species were both significant ($B_c = -92.98 + 15.81$ total number of species $+ 26.40$ average age, $P < 0.01$, $r^2 = 0.76$). The standardized regression coefficients, 0.83 and 0.38, indicated that average age provided a greater contribution to estimating biomass than the total number of species. Eliminating Black and Carruthers lakes, two lakes that seemed to have unusually high biomass values (Table 4; Fig. 2), did little

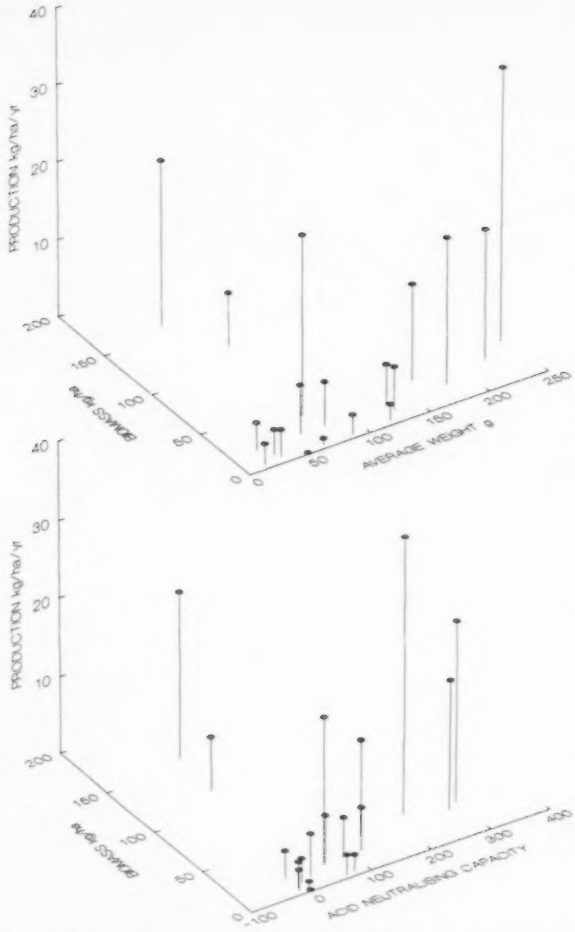

FIG. 4. Relationships among production (P_c), biomass, average weight of individuals, and ANC for all fish in 19 lakes from four watersheds in north-central Ontario.

to change the relationship ($r^2 = 0.79$; Fig. 3). When we included ANC and lake morphometric characteristics with number of species, and average age and weight, only the total number of fish species and average age were significant in the multiple regression. Therefore, we concluded that biomass was a function of the number of species in the community and their age (and presumably size). Lake morphometry and chemistry, including pH, ANC, and total phosphorus, of these 19 lakes were not significantly related to whole-lake fish biomass.

We used a similar approach to examine the relationships of biological and lake characteristics to whole-lake fish production. Lake fish production (P_c) was not significantly different (ANOVA, $F = 1.01$, not significant) among the four communities (Fig. 1) identified by cluster analysis. The stepwise regression identified only average weight ($P < 0.05$) as being significantly related to P_c. The multiple regression using average weight, biomass, and ANC (Fig. 4) was significant ($P_c = 1.40 + 0.09\ B_c + 0.05$ ANC $+ 0.05$ average weight). The standardized regression coefficients (0.40, 0.46, and 0.33, respectively, from the regression equation) indicated that their

contributions to the regression were approximately similar (Fig. 4).

In summary, the biomass of fish in our lakes appeared to be related to the number of species (slightly greater biomass with more species) and the average age (older, presumably larger, fish contributed greater biomass) of the populations. The increase in fish community biomass contributed by more than a few (less than three) species was small, however. Community fish production, on the other hand, was more variable and was a function of not only the biomass and average size of fish in the community but also lake ANC. It appeared that the effects of ANC and/or pH on fish production resulted from both a lower fish size at lower ANC and a variable but often lower growth rate at lower ANC.

Discussion

The limits to our understanding of the effects of acidic deposition on aquatic biomass and productivity were reviewed by Dillon et al. (1984). Case histories documenting changes in fish abundance or production are few (an exception being, perhaps, Lumsden Lake, Beamish and Harvey (1972)). This scarcity of time series data for B_c and P_c as lakes have acidified (Kelso et al. 1990) makes empirical analysis over a gradient of vulnerability and severity of impact to acidic atmospheric deposition the next best experimental approach. Downing et al. (1990) did not find any correlation between pH and fish production in estimates available in the primary literature. Our data for 19 lakes on the Canadian Shield are therefore unique, as we estimated B_c and P_c and were able to evaluate some of the factors which were expected to influence them. Our lakes, by design, were selected to remove much of the effects of lake morphometry, temperature, and probably nutrients, thus holding some factors constant and removing a characteristic of the data used by Downing et al. (1990). We maximized the differences among lakes in terms of their susceptibility to acidification, and to do this, we had to select lakes in different watersheds, thus imposing some differences in fish community structure. Further, while abundance was estimated using different methods, we selected the best method for each circumstance. The field methods also minimized biases and maximized adherence to underlying assumptions for population estimation (Ricker 1975).

There are clearly differences in fish community structure among these lakes and watersheds (M. G. Johnson, J. R. M. Kelso, and C. K. Minns, unpubl. data) although three watersheds had communities with mixtures of centrarchids and yellow perch. Also, while fish communities differed among our lakes and only acid-tolerant species (yellow perch, pumpkinseed, and brown bullhead) were present in the low-pH lakes, the number of fish species was not statistically related to lake pH in our data set. With the exception of central mudminnow (*Umbra limi*), the fish species in our lakes are those commonly found in acid-sensitive lakes (Matuszek et al. 1988). Our lake selection procedure may have reduced the possibility of species–pH and species – lake area relationships and selected for lakes with ubiquitous, acid-tolerant fish species only.

Regardless of what fish species were present, few species (often one, always fewer than three) contributed >75% to the total fish biomass (B_c) of a lake. Adams and Olver (1977) and Fraser (1981) attributed the relatively large contribution by a few species (yellow perch and white sucker, in their cases) to fish yield to be characteristic of fish communities. Consequently, the large contribution by only a few fish species to B_c (yellow perch, white sucker, brook trout, and several centrarchid species in our case) is likely to be an inherent property of aquatic systems and can be fulfilled by any generalist species. In small lakes where fish species tend to be fewer and habitat diversity less, it would probably be easier for generalist species to dominate fish communities. Kolasa and Strayers' (1988) habitat-based model supports this contention, as the abundance of specialist fish species (e.g. some acid-sensitive cyprinids) would be constrained, thus limiting their abundance and biomass. It appears that, regardless of the mechanisms that establish or the factors that subsequently affect community structure, most of the biomass appears confined to only a few fish species. In these lakes, unlike the studies identified in the introduction, fish communities could not be characterized by lake characteristics (we found, largely, watershed differences) and the number of fish species present was not significantly related to pH.

In our measurement of biomass in these Shield lakes, two lakes, Black and Carruthers, had high biomass (> 100 kg/ha). When viewed in light of their community structure and the biological characteristics of those communities, these lakes are not unusual; that is, their high biomass results from more species which provide incremental, but declining, increases to B_c, a preponderance of older individuals, and generally low G_x. When viewed only in relation to lake physical/chemical properties (Fig. 2), the high biomass appeared anomalous. While we can partly explain these high biomasses, we also suggest that the communities in these two lakes may have been perturbed (access is easy; new species may have been introduced; an existing species may have increased in abundance or been stressed) and their communities may be in the process of restructuring. If these two lakes are excluded from the analysis, lake B_c is significantly related to the number of fish species present and their average age, as well as to ANC. Our range in fish community annual production, from approximately 1 to 35 $kg \cdot ha^{-1} \cdot yr^{-1}$, was similar to that partially summarized by Kelso (1985) but at the low end of the range identified by Downing et al. (1990). Unlike the findings of Downing et al. (1990), whole-lake fish production, P_c, was significantly related to B_c (by definition and calculation), average weight of the fish present, and lake ANC.

As B_c was not consistently related to ANC (the relationship was significant only when Black and Carruthers lakes were excluded from the analysis), the relationship between P_c and ANC (or pH) arose in our lakes largely from differences in G_x and fish size. Fish growth and condition factor have been shown to respond in both a lake-specific and species-specific manner (summarized by Dillon et al. 1984; Kelso et al. 1990). In our lakes, G_x was less at lower pH for white sucker, and it appears that population growth may have been generally slower at lower pH. Unfortunately, we were able to test the relationship of pH with G_x for only the few species that occurred in sufficient lakes.

Matuszek and Beggs (1988) indicated that an understanding of the interactions among lake physical characteristics and species richness was essential to explain the role of pH or ANC effects upon fish species richness. The concern of Matuszek and Beggs applies also to understanding the relative influence of pH (or ANC) and fish community structure upon biomass and production. While both B_c and P_c were lower at low lake ANC, they were more clearly related to species-specific attributes such as the age, size, and growth rates of the fish present. Schell and Kerekes (1989) suggested that macroinvertebrate abundance and biomass were related to nutrient availability

rather than acidity in lakes of Nova Scotia. Consequently, we believe that empirical models of yield, B_c, and P_c will become more robust when factors relating to fish community structure and to lake productive capacity are better known.

From our lakes (and Downing et al. 1990), there was no apparent relationship between fish species richness and lake pH (and lake trophic status). On the other hand, fish community biomass was significantly related to the total number of species, their average age, and perhaps to lake ANC. As a result, we would expect B_c to be reduced by small increments during lake acidification as long as species remain. Fish community production, however, was more clearly related to lake ANC mainly through relation of growth rates with lake ANC. Thus, P_c is more likely to be noticeably reduced by the occurrence of lake acidification. Fish community restructuring, or compensation within the community, that might occur during lake acidification still remains a critical factor in any evaluation of changes in fish biomass and production from resource perturbation.

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PERSPECTIVES

Further Perspectives on Yield per Recruit Analysis and Biological Reference Points

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Norris, J. G. 1991. Further perspectives on yield per recruit analysis and biological reference points. Can. J. Fish. Aquat. Sci. 48: 2533–2542.

Spawner–recruit relationships (SRRs) are indeterminate for most species. Earlier workers proposed solving "amount of harvest" problems for such cases by tacitly assuming that the SRR is density independent (a straight line through the origin) for the available data. I extend that concept and demonstrate a technique for solving "method of harvest" problems when the SRR is indeterminate. This technique uses spawning biomass per recruit, rather than fishing effort, as the benchmark for comparing alternative methods of harvest. Yields from different harvesting methods are deemed comparable only when they produce the same spawning biomass per recruit. If the comparisons are consistent over the entire range of spawning biomass per recruit values, one can evaluate the relative merits of competing methods of harvest without the benefit of spawner–recruit data. Although this technique does not determine the optimal gear selectivity, it allows comparisons of sustainable yields from currently available gear types. The technique is particularly useful for analyzing fishery allocation and by-catch problems. Two life history parameters, critical age (age at which a cohort maximizes its biomass or dollar value) and the age at 50% sexual maturity, may be most important in determining the optimal method of harvest (fishing gear selectivity).

La relation géniteur–recrue (RGR) n'est pas connue pour la plupart des espèces. Des chercheurs ont déjà proposé de résoudre les problèmes de « quantification des récoltes » pour ces espèces en supposant implicitement que la RGR était indépendante de la densité (une droite qui passe par l'origine) pour les données dont ils disposaient. Je pousse plus loin ce concept et je décris une technique pour résoudre les problèmes de « méthodes de récolte » lorsque la RGR est inconnue. Cette technique fait appel à la biomasse de géniteurs par recrue plutôt que par effort de pêche comme point de référence pour comparer diverses méthodes de pêche. Ainsi, les rendements de différentes méthodes de récolte ne sont réputés comparables que lorsque les biomasses de géniteurs par recrue sont identiques. Si les comparaisons sont cohérentes pour l'ensemble des valeurs de biomasse de géniteurs par recrue, il est alors possible d'évaluer les avantages relatifs de différentes méthodes de récolte sans avoir recours aux données sur la relation géniteur–recrue. Bien que cette technique ne permette pas de déterminer la sélectivité optimale des engins de pêche, elle permet des comparaisons entre les rendements soutenus des différents engins de pêche utilisés actuellement. Cette technique est particulièrement utile pour analyser les problèmes liés aux allocations de pêche et aux prises fortuites. Deux paramètres du cycle biologique, l'âge critique (âge auquel une cohorte a une biomasse ou une valeur en dollar maximale) et l'âge correspondant à 50 % de la maturité sexuelle, peuvent être très importants pour déterminer la méthode de récolte optimale (sélectivité des engins de pêche).

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Single-species fishery management problems can, for the most part, be divided into two groups: (1) "amount of harvest" problems (How many fish should be caught?) and (2) "method of harvest" problems (What fish should be caught?). Amount of harvest problems deal with controlling fishing effort (F) to achieve certain operational objectives, such as maximizing yield per recruit ($F = F_{max}$), maximizing long-term yield ($F = F_{msy}$), minimizing the effects on future recruitment while promoting economic efficiency ($F = F_{0.1}$), or preventing "recruitment overfishing" ($F < F_{ro}$), which occurs when the spawning biomass is reduced to a point where recruitment declines rapidly, or fails altogether (Sissenwine and Shepherd 1987). Method of harvest problems deal with finding the best age- or size-specific harvesting method. A method of harvest can be defined to be a set of age- or size-specific gear selectivity coefficients. If several gear types, each with different selectivity characteristics, are available to harvest a particular species, a method of harvest is defined by the amount of the total fishing effort apportioned to each gear type. Thus, method of harvest problems often manifest themselves as "allocation problems" or "by-catch problems." Although method of harvest problems are less common than amount of harvest problems, they often generate considerable political controversy and concomitant headaches for fishery managers.

Beverton and Holt (1957) popularized the use of yield per recruit analysis (dynamic pool models) to provide scientific advice on solving both types of problems. Their technique assumes that management has only two control variables: (1)

total fishing effort (F) and (2) the age at which capture should begin (t_c). Finding the appropriate F is an amount of harvest problem, while finding the appropriate t_c is a method of harvest problem. The basic principle of yield per recruit analysis is that the per capita harvestable yields (e.g. biomass or dollars) from a cohort of fish over its fishable life span are functions of three processes: fishing mortality, survival, and growth. If the fishing mortality, survival, and growth rates are constant for enough time to influence all cohorts within the population and if recruitment is fairly constant, the population will approach an equilibrium condition (i.e. stationary age distribution) and the yield from a single cohort over its fishable life span will equal that of the total population in a single year. In addition to biomass and dollar yields, a cohort of fish also produces an egg yield that is a function of the egg production process as well as the three processes mentioned above. Since increasing biomass and dollar yields generally result in a decreasing egg yield, egg yield is most often viewed as a constraint rather than a yield. That is, we take biomass and dollar yields from a stock only so long as the egg yield is sufficient to provide adequate recruitment in future years.

A variety of methods have been described for combining dynamic pool and spawner–recruit models (Getz 1979; Reed 1980; Shepherd 1982; Deriso 1987), but these methods have little applicability unless the spawner–recruit relationship is well defined. Sissenwine and Shepherd (1987) demonstrated how spawner–recruit data can be combined with a dynamic pool model to provide scientific advice on amount of harvest problems even though the underlying spawner–recruit relationship is indeterminate. The purpose of this paper is to extend their perspective by demonstrating how dynamic pool models can be used to provide scientific advice on method of harvest problems in a reproductively meaningful way when the spawner–recruit relationship is unknown.

The paper is divided into four sections. First, I review some of the theoretical results from single-species yield theory. Second, I describe a procedure for comparing different methods of harvest when the stock–recruit relationship is indeterminate. Third, I apply the procedure to the sablefish (*Anoplopoma fimbria*) fishery off the coasts of Washington, Oregon, and California. Fourth, I discuss the limitations and possible uses of the procedure.

Theoretical Results from Single Species Yield Theory

Traditional yield per recruit analysis compares alternative harvesting strategies by fixing F and solving the yield integrals for different values of t_c, or vice versa. Until recently, most researchers employing yield per recruit analysis simply avoided considering any reproductive constraints by assuming that recruitment is constant and independent of stock size, even though it was known that this assumption could lead to unacceptable policy recommendations. For example, when fishing effort is age specific and unlimited, the optimal harvesting strategy from a yield per recruit analysis is to take all of the harvest at the "critical age" at which the cohort reaches its maximum biomass or dollar value (Ricker 1975). The implication of this result is that commercial fishing gears should be designed to allow escapement of all fish younger than the critical age and effort should be unlimited. If the critical age is younger than the age of sexual maturity, such a fishery is obviously not sustainable.

Getz (1979) and Reed (1980) incorporated an egg–recruit relationship into a yield per recruit model and solved for the age-specific harvesting policy that maximizes yield. Their solution was useful because it proved that the optimal harvesting policy must assume one of only three possible forms: (1) a partial harvest at one intermediate age with no further harvesting, (2) a partial harvest at one intermediate age followed by a total harvest at one later age, and (3) a total harvest at one age. Reed (1980) also proved that if the egg–recruit relationship does not involve overcompensation (i.e. if recruitment never decreases as egg production increases), then the optimal harvesting policy will not involve harvesting before the critical age defined by Ricker (1975). Lovejoy (1986) extended this conclusion to the stochastic case.

The solution for the Arcto-Norwegian cod example presented by Reed (1980) deviated from conventional wisdom because it involved harvesting only immature fish. For Arcto-Norwegian cod the critical age is 6, the age of first sexual maturity is 7, and the optimal harvesting policy determined by Reed (1980) was to harvest 44.6% of the age 6 animals with no other harvest. He also showed that a less selective policy that harvests ages 5–8 gives almost as much yield as the optimal policy and gives a higher yield than policies using only a minimum age control. Thus, in some cases, the optimal harvesting strategy is a partial harvest of the young, fast-growing, sexually immature individuals while saving old, slow-growing individuals for egg production. Although the optimal solutions given by the Getz–Reed approach may be unrealistic for fisheries in which the available gears are not selective enough to harvest individual age classes within a stock, in cases where gears are, in fact, more selective for immature fish, the benefits derived by using such gears, in terms of saving older fish for reproduction, will not be identified through a traditional yield per recruit approach.

Botsford and Hobbs (1986) offered a slightly different approach to the problem of accounting for reproductive potential in a yield per recruit analysis. They assumed that spawning biomass per recruit must be held at some arbitrarily determined "safe" level and then solved the problem of finding the combination of minimum and maximum age limits and fishing effort level that both maximizes economic yield and satisfies the spawning biomass per recruit constraint.

Shepherd (1982) illustrated how a spawner–recruit relationship can be combined with a dynamic pool model to generate sustainable yield curves as a function of fishing effort. Each sustainable yield curve generated by this method is dependent on t_c, and therefore this method ignores the problem of finding the best age-specific method of harvest.

In practice, the Getz–Reed, Botsford–Hobbs, and Shepherd approaches suffer from the same problem, namely that of identifying the correct egg–recruit relationship or the "safe" spawning biomass per recruit level. Sissenwine and Shepherd (1987) suggested that an appropriate definition of a "safe" level would be the number of eggs (or spawning biomass) produced by a cohort over its lifetime that is, on average, equal to that produced by its parents. If egg production fell below that level more often than above it, the population would decline. They denoted the level of fishing effort (conditional on t_c) that corresponds to average replacement as F_{rep}. In practice, F_{rep} is estimated by assuming that the distribution of the spawner-recruit relationship is density independent and stationary and, therefore, expected recruitment can be represented by a linear function through the origin (see fig. 2 in Sissenwine and Shepherd 1987).

This method is "safe" in the sense that it determines a level of fishing effort that will maintain recruitment at some equilibrium level (on average). However, because the underlying spawner–recruit relationship is indeterminate, one is left with the problem of determining the relationship (i.e. relative values) between F_{rep} and other biological reference points, such as $F_{0.1}$, F_{msy}, and F_{ro} illustrated in fig. 1 of Sissenwine and Shepherd (1987). Figure 1 in this paper is modified from Sissenwine and Shepherd (1987) and illustrates the case where the underlying spawner–recruit relationship is an asymptotic function and F_{rep} is estimated from two sets of data. Dataset A represents a developing fishery in which stock size is relatively large and $F_{rep} < F_{msy}$. Dataset B represents an established, overexploited fishery in which spawner-recruit data are collected only after the stock abundance has been reduced to relatively low levels and leads to $F_{rep} > F_{msy}$. In both cases, F_{rep} is "safe" in the sense that the stock will continue to replace itself, but neither is optimal because F_{rep} does not equal F_{msy}. Further, it is possible that $F_{rep} > F_{ro}$ when estimated from dataset B.

Figure 1 illustrates the importance of knowing where on the underlying spawner–recruit relationship one's data points lie before drawing conclusions about the consequences of a given level of fishing effort. The essence of the Sissenwine and Shepherd approach is to utilize only spawner–recruit data that are thought to provide a reasonable linear approximation of the steep ascending portion of the spawner–recruit relationship. However, their statement "For a population to persist, the points below the [estimated average replacement] line must be balanced by the points above it," while technically correct in the absence of density dependence, is somewhat misleading in that it might be construed to mean that the population will always collapse if $F > F_{rep}$. When density dependence is present, this may not be the case, as Fig. 1 illustrates. The fact remains that when density dependence is present, each level of fishing effort (F) has an associated equilibrium stock abundance. In these cases, F_{rep}, as estimated by the Sissenwine–Shepherd approach, is highly dependent on the range of stock abundances for which spawner–recruit data are available. Without further knowledge of the underlying spawner–recruit relationship, it is difficult to conclude that a level of fishing effort greater than F_{rep} will in fact lead to a precipitous decline in recruitment. Sissenwine and Shepherd's suggestion to employ an adaptive management strategy (Walters 1986) for developing fisheries when F_{rep} is likely to be conservative (i.e. $F_{rep} < F_{ro}$) is equally applicable to situations where F_{rep} could possibly be too large (e.g. case B in Fig. 1). There simply is no substitute for learning more about the dynamics of the recruitment process.

Comparing Methods of Harvest when the Spawner–Recruit Relationship Is Indeterminate

The theoretical results from Getz (1979) and Reed (1980) indicate that the yield from a fishery is determined by a complex interaction between amount of harvest (i.e. fishing effort), the method of harvest (i.e. gear selectivity), the life history parameters of the species in question (i.e. growth, natural mortality, and egg production), and the underlying spawner–recruit relationship. Further, the Arcto-Norwegian cod example given by Reed (1980) demonstrated that under certain conditions it is possible for a counterintuitive harvesting strategy (e.g. a partial harvest of sexually immature fish with no further harvesting) to give maximum sustainable yield. As we shall see in the example, the degrees to which different methods of harvest affect the reproductive potential of the stock can become a subject of heated political debate when the stock must be allocated among different gear types. For most fisheries, gear selectivity coefficients and life history parameters can be estimated through appropriate research. However, identification of a spawner–recruit relationship has been next to impossible. Thus, it would be helpful to have a procedure for comparing different methods of harvest that accounts for their respective effects on reproductive potential.

Figure 2 is modified from Sissenwine and Shepherd (1987) and illustrates the problem of comparing two harvesting strategies (labeled H_1 and H_2) that have different yield per recruit and spawning biomass per recruit functions. Although strategy H_2 has a lower yield per recruit for a fixed level of fishing effort (F), it has a higher spawning biomass per recruit and higher total equilibrium recruitment. Since total yield is the product of the yield per recruit and total recruitment, any comparison of equilibrium total biomass yields is indeterminate without knowledge of the spawner–recruit function. Whether one harvesting strategy is better than the other depends on the relative benefit of the increase in recruitment compared with the loss in yield per recruit.

When spawner–recruit data are available but too variable to fit a spawner–recruit function, the Sissenwine–Shepherd method for estimating F_{rep} could be used to compare yields from different methods of harvest (Fig. 3). The solid replacement line in Fig. 3c corresponds to F_{rep} values for each harvesting method in Fig. 3a. For the example shown, the corresponding yields in Fig. 3d indicate that harvesting method H_2 gives the higher yield and should be preferred. If no spawner–recruit data are available to identify a single replacement line, one can proceed by comparing yields over all possible replacement lines, represented by the broken replacement lines in Fig. 3c. Since each possible replacement line corresponds to a unique level of spawning biomass per recruit, this procedure is identical to plotting yield per recruit against spawning biomass per recruit. If the yield comparisons are consistent over the entire range of spawning biomass per recruit values (i.e. if one harvesting method has higher yield for all spawning biomass per recruit values), the preferred harvesting method can be identified. As we shall see in the example, yield comparisons are not always consistent and a preferred harvesting method cannot always be identified.

As a practical matter, plotting yield per recruit against spawning biomass per recruit is fairly simple. Spawning biomass per recruit and corresponding yield per recruit values are determined by evaluating the yield and spawning biomass per recruit integrals over a broad range of fishing effort levels.

This approach is essentially identical to that of Botsford and Hobbs (1986), the main difference being in the presentation of the results. They used separate graphs (with the same coordinates) to illustrate the combinations of lower size limit and fishing mortality rate that satisfy (1) different values of the constraint equation (their fig. 1) and (2) the solutions to the biomass or dollar yield integrals as the value of the egg yield constraint changes (their fig. 2). They suggested that managers can overlay the two graphs and "by following the line along which k [spawning biomass per recruit] varies can observe the way in which the optimal fishing mortality rate and size limit change as the relative importance to reproduction is subjectively varied."

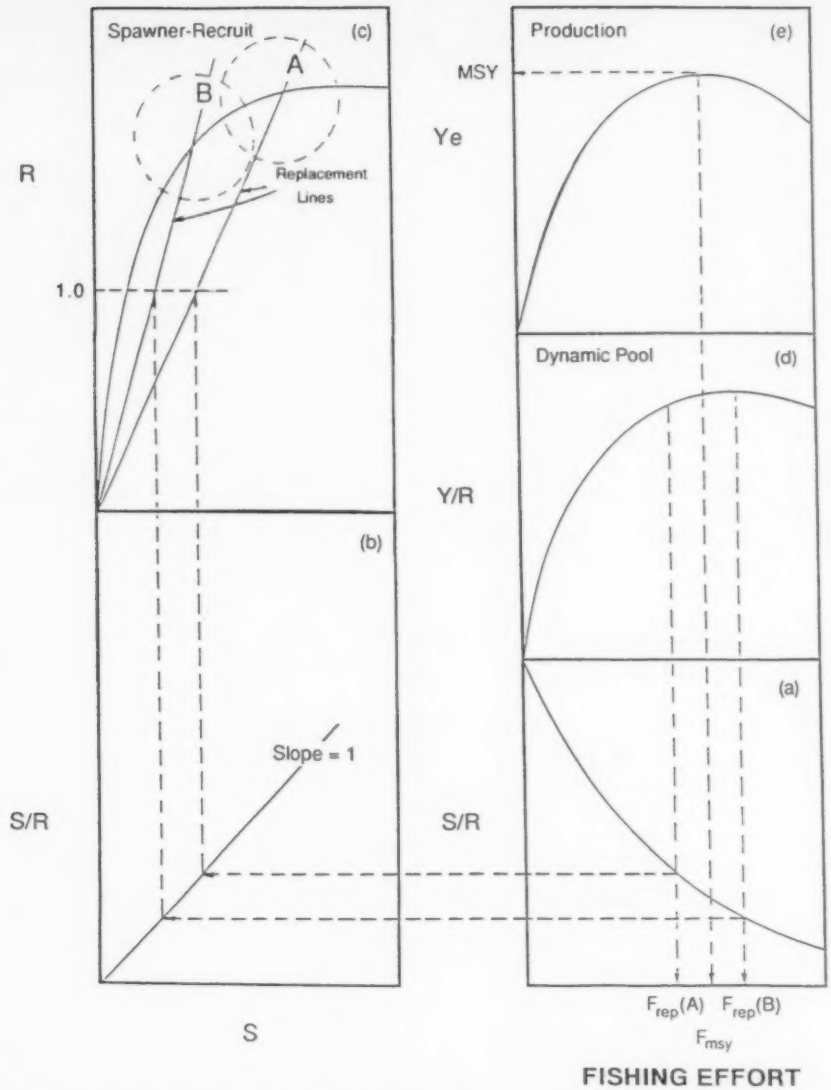

FIG. 1. Single-species theory of fishing and the Sissenwine–Shepherd method of estimating F_{rep} from two sets of spawner–recruit data (A = developing fishery; B = established, overexploited fishery). A dynamic pool model (Fig. 1a and 1d) describes the effect of fishing effort on spawning biomass (S) per recruit (R) and yield (Y) per recruit. A spawner–recruit model (Fig. 1c) relates the number of recruits to spawning biomass; a "replacement line" with slope equal to the inverse of S/R is mapped by a graphic procedure (Fig. 1b). S and R must be scaled to appropriate units (e.g. thousands of tons and millions of fish, respectively) in order for the graphic procedure to be practical. The intersection of the replacement line with the spawner–recruit function determines equilibrium recruitment. The product of equilibrium recruitment (from Fig. 1c) and yield per recruit (from Fig. 1d) is the equilibrium production (Fig. 1e). Both datasets lead to estimates of F_{rep} that are "safe" in the sense that the stock will continue to replace itself, but neither is optimal because F_{rep} does not equal F_{msy}. Thus, it is important to know where on the spawner–recruit function one's data points lie before drawing conclusions about the consequences of a given level of fishing effort. (Adapted from Sissenwine and Shepherd 1987)

The approach I am suggesting is more pragmatic. I assume that the manager has only a few realistic methods of harvest he wishes to compare (defined by current gear technology and political milieu), and then uses a single graph that plots yield per recruit for each method as a function of spawning biomass per recruit. In this way, harvesting methods are compared in a biologically meaningful manner. It should be noted that yield can be measured in terms of biomass or dollars and that eggs per recruit could be substituted for spawning biomass per recruit.

My discussion thus far has focused on spawning biomass (or egg production) as the most important characteristic of the spawning stock in determining recruitment. Other character-

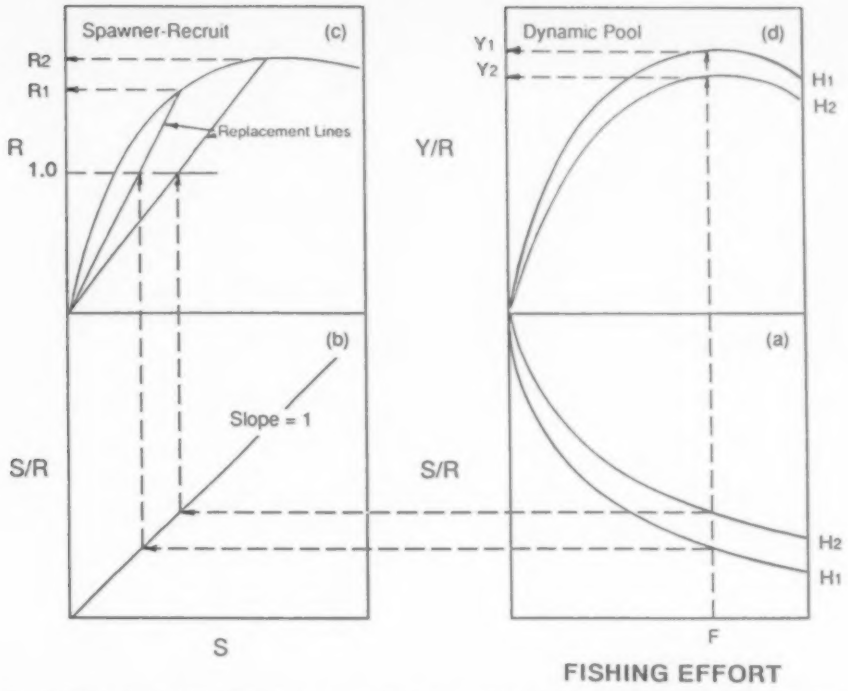

FIG. 2. Illustration of the difficulty in comparing two methods of harvest (labeled H_1 and H_2) when fishing effort is used as the benchmark for comparison. Although harvest method H_1 has a higher yield per recruit (Y_1), it has a lower egg yield per recruit which results in lower equilibrium recruitment (R_1). Since total equilibrium yield is the product of equilibrium recruitment and yield per recruit, a comparison of total equilibrium yields from the two methods of harvest (i.e. $Y_1 \cdot R_1$ versus $Y_2 \cdot R_2$) is indeterminate.

istics may be equally important. For example, Leaman and Beamish (1984) suggested that for long-lived species that are dependent on sporadic large year classes, managers also should consider the age structure of the spawning stock, not only how many eggs it produces. They argued that a spawning stock composed of many age classes may be required to withstand a prolonged series of recruitment failures caused by unfavorable environmental conditions. A stock may collapse if too few age classes are present, as has been argued for the California sardine (*Sardinops caerulea*) fishery (Murphy 1966).

The method proposed here permits the age and size structures of the spawning stocks generated by each method of harvest to be compared at selected levels of spawning biomass per recruit. As we shall see in the example, methods of harvest that produce the same spawning biomass per recruit may have somewhat different age structures in the spawning stock. If the number of age classes contributing to egg production is important to the manager, as Leaman and Beamish (1984) suggested it should be, then these characteristics can also be examined.

To summarize, this analysis approach consists of four steps:

Step 1. Develop a dynamic pool model of the fishery, including estimates of gear selectivity.

Step 2. For each method of harvest, calculate yield (biomass or dollars) and spawning biomass (or eggs) per recruit over a broad range of fishing effort levels.

Step 3. Compare methods of harvest by plotting yields (biomass or dollars) per recruit as functions of spawning biomass (or eggs) per recruit.

Step 4. Compare spawning stock and population characteristics associated with each method of harvest at specific spawning biomass (or eggs) per recruit levels of interest.

An Example

Sablefish along the coasts of Washington, Oregon, and California (WOC area) have been harvested by four types of fishing gear: trawls, traps, longlines, and set-nets. Trawls and traps are most selective for smaller, sexually immature fish whereas longlines and set-nets are most selective for larger, sexually mature fish (Fig. 4). Nontrawl gears receive higher prices; for all gear types, premiums are paid for larger fish (Table 1). No spawner–recruit relationship has been determined for this stock.

A difficult management problem for the Pacific Fishery Management Council has been the allocation of the sablefish Acceptable Biological Catch among the trawl and nontrawl gear types. The effect each gear type has on the reproductive potential of the stock has been a subject of considerable controversy. Trawl fishermen argue that nontrawl gears have a negative impact on the spawning stock because they harvest a disproportionate number of large, highly fecund females. Nontrawl fishermen argue that because trawl gear harvests mostly small, immature, and less valuable fish, it not only has a negative impact on the future spawning stock, but also generates suboptimal yields.

Without a well defined spawner–recruit relationship, it has been difficult to determine the preferred harvesting method. In fact, the theoretical results from Getz (1979) and Reed (1980) suggest that any one of the four gear types might provide the optimal age-specific harvesting method. For example, since trawl selectivity declines as fish size increases, a trawl-only harvesting strategy is similar to the theoretical case where the

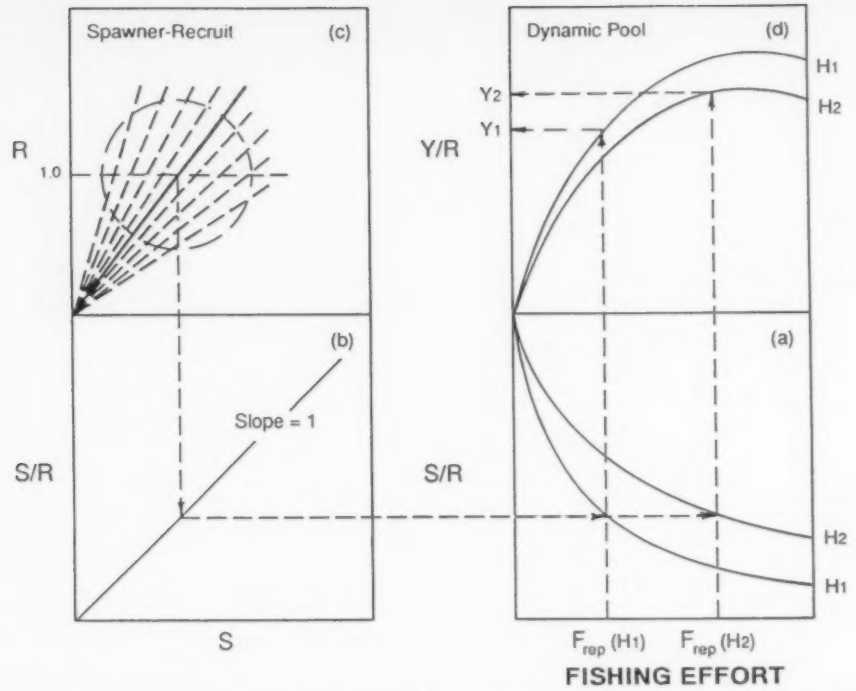

FIG. 3. Two procedures for comparing methods of harvest (H_1 and H_2) when a spawner–recruit relationship cannot be identified. (1) If spawner–recruit data are available but too variable to identify a spawner–recruit relationship, a single replacement line (solid line in Fig. 3c) and corresponding yields per recruit (Y_1 and Y_2) can be estimated using the techniques of Sissenwine and Shepherd (1987). In the example shown, harvesting method H_2 gives the highest yield. (2) If no spawner–recruit data are available, yields per recruit for each method of harvest can be plotted against a broad range of spawning biomass per recruit values. This procedure is identical to considering all possible replacement lines (broken lines in Fig. 3c) that might realistically be estimated from future data.

optimal policy involves a partial harvest at one intermediate age, with no further harvesting (e.g. the Arcto-Norwegian cod case from Reed 1980). Conversely, since longline selectivity increases as fish size increases, a longline-only harvesting strategy is similar to the theoretical case where the optimal policy is a total harvest at one age. Since no spawner–recruit function has been identified for sablefish, the Getz–Reed methodology cannot be used to determine which type of gear selectivity will produce the greatest sustainable yields.

I developed a dynamic pool model of the sablefish fishery in Norris (1989). In addition to the gear selectivity functions illustrated in Fig. 4, the model incorporated a simple technique for adding more structure to the individual growth process. This added growth structure was needed because the longline and set-net gears were highly selective for sizes that were larger than the asymptotic maximums of the von Bertalanffy growth functions for each sex. Age–length data were used to define, for each sex, a family of von Bertalanffy growth curves that have the same k and t_0 parameters, but which have L_∞ parameters described by a probability distribution. The population was then partitioned into 10 subgroups (five for each sex) based on growth (Fig. 5). Selectivity and recruitment were treated as separate processes. For sablefish, recruitment occurs as young fish migrate from unexploitable inshore nursery areas to the continental shelf and slope where they become vulnerable to the commercial fishery (McFarlane and Beamish 1983). I used a logistic function based on age to model the recruitment process. In addition to calculating yields, the model kept track of the age–frequency and length–frequency distributions of the total population, the exploitable population (defined to be the portion of the total population that has recruited to the fishing grounds), the spawning stock (females only), and the catches by each gear type. Population and catch statistics were calculated from these distributions.

I chose to plot yields against number of eggs produced, rather than spawning biomass, because for sablefish, I found that different levels of spawning biomass produced different numbers of eggs. The source of this difference was in the exponents of the power functions used by the model to describe the length–eggs relationship (exponent = 2.8244) and length–weight relationship (exponent = 3.12219). As sablefish grow in length they increase their weight faster than they increase their egg production. Thus, the same biomass of small fish produces more eggs than an equal biomass of large fish.

Yields from six possible harvesting methods were compared: (1) trawl only, (2) adjusted trawl only (exvessel prices set at longline values), (3) trap only, (4) longline only, (5) set-net only, and (6) mixed gear (simulated the 1988 fishery which allocated 56 and 44% of the catch to trawl and nontrawl gears, respectively). Although the biomass yields per recruit were nearly identical at all eggs per recruit values, the dollar yields per recruit for the nontrawl strategies were about 2.4 times

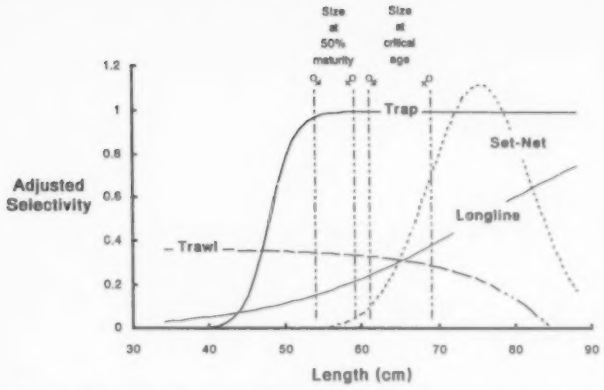

FIG. 4. Sablefish adjusted selectivity functions (gear selectivity times relative efficiency) for commercial trawl, trap, longline, and set-net gears (from Norris 1989). For each gear type, relative selectivity is defined to be the fraction of fish in a given size class that are retained by the fishing gear once they encounter it. Relative efficiency adjusts the efficiency of each gear type with respect to a standardized gear (trap gear in this example). Vertical lines reference mean individual lengths at 50% sexual maturity (54-cm males; 59-cm females) and at critical ages when the population reaches maximum dollar value (61-cm males; 69-cm females).

TABLE 1. Average exvessel prices ($/kg round weight) in Washington State during 1984–86 (source: Washington Department of Fisheries fish ticket data).

Market size category	Trawl	Trap	Longline	Set-net
Larve (over 3.17 kg)	0.713	1.624	1.443	1.306
Medium (2.27–3.17 kg)	0.556	1.295	1.246	1.209
Small (under 2.27 kg)	0.454	0.920	0.865	0.977

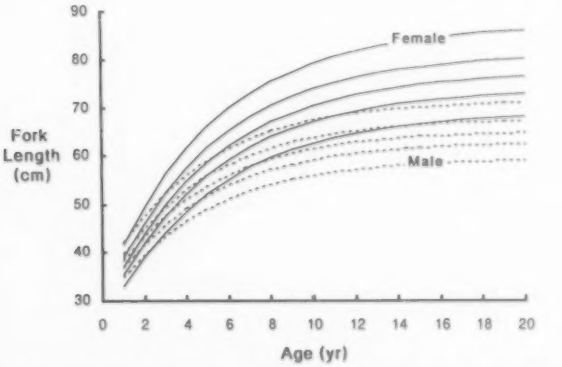

FIG. 5. Male (broken lines) and female (solid lines) von Bertalanffy growth functions used in the dynamic pool model of the sablefish stock in the WOC area. Within each family of curves (male and female), the k and t_0 parameters are the same, but the L_∞ parameters are selected from a probability distribution such that each curve is centered on the 10th, 30th, 50th, 70th, and 90th percentiles of the population.

larger than the trawl-only strategy and about 1.6 times larger than the mixed gear strategy (Fig. 6).

The reason for the higher dollar value of the nontrawl fisheries is that trawls catch smaller, lower valued fish and regardless of size, trawl-caught fish are of lower value (Table 2). When eggs per recruit is fixed at 226 000 eggs (the average level I estimated for the period 1976–85 for the Washington coast fishery), mean individual weights in the trawl and longline catches are 2.02 and 2.71 kg/fish, respectively. Even when trawl gear receives longline prices (adjusted trawl strategy), the longline dollar yield is about 16% greater due to the higher premiums paid for larger fish.

The selective properties of the gears also affect the size structure of the total and exploitable populations, the exploitation rate (defined to be harvested biomass divided by exploitable biomass), and the spawning biomass (Table 2). For example, as gear selectivity favors larger fish (e.g. set-net versus trawl), the biomass of the exploitable population increases (12 789 versus 8927 kg) but is composed of smaller fish (2.15 versus 2.32 kg/fish). The exploitation rate was lower when larger fish were harvested (e.g. 0.072 for set-net versus 0.108 for trawl). Also, the spawning biomass needed to produce 226 000 eggs per recruit was slightly lower when larger fish were harvested (e.g. 4326 kg for set-net versus 4454 kg for trawl).

All methods of harvest result in a considerable loss of older age classes in the spawning stock (Fig. 7). As the fishing gear becomes more selective for larger fish, the age structure of the spawning stock becomes more concentrated around the younger age classes. Trawl gear gives a more favorable age structure to the spawning stock, in terms of including more age classes, than do the other single gear strategies. However, without better knowledge of the factors influencing recruitment variability, it is difficult to evaluate the significance of the differences in spawning stock age structures associated with different harvesting strategies.

Discussion

For the sablefish example, my results indicate that the benefits of a lower fishing mortality on larger spawning females are not sufficient to give the trawl-only strategy higher yields. Since all of the nontrawl strategies have significantly higher dollar yields per recruit than the trawl-only strategy over the entire range of egg yield per recruit values, one can conclude that nontrawl harvesting strategies will most likely result in higher exvessel dollar yields than does a trawl gear harvest, regardless of the spawner–recruit relationship.

In terms of the theoretical results from Reed (1980), the optimal age-specific harvesting strategy for sablefish appears to be a total harvest at one age (past the age of sexual maturity), rather than a partial harvest at some intermediate age, as was the case for Arcto-Norwegian cod. An important difference between these two species is the relationship between the critical age and the age at 50% maturity. For Arcto-Norwegian cod, the critical age is considerably younger than the age at 50% maturity, thus making it possible for the optimal policy to involve harvesting young immature fish. For sablefish, the critical ages for biomass and dollar values are 6.9 and 9.0 yr, respectively (Norris 1989), both of which are older than the age at 50% maturity (5 yr). Thus, for sablefish, a strategy that harvests young, immature individuals is not optimal because the fish have not reached their full growth potential.

The importance of the relationship between the critical age and the age at 50% maturity can be demonstrated simply by changing the sablefish age at 50% maturity parameter from 5 to 12 yr. With this single adjustment in the life history parameters, the trawl-only strategy produces a yield per recruit that is about 15% greater than that for a longline-only harvest

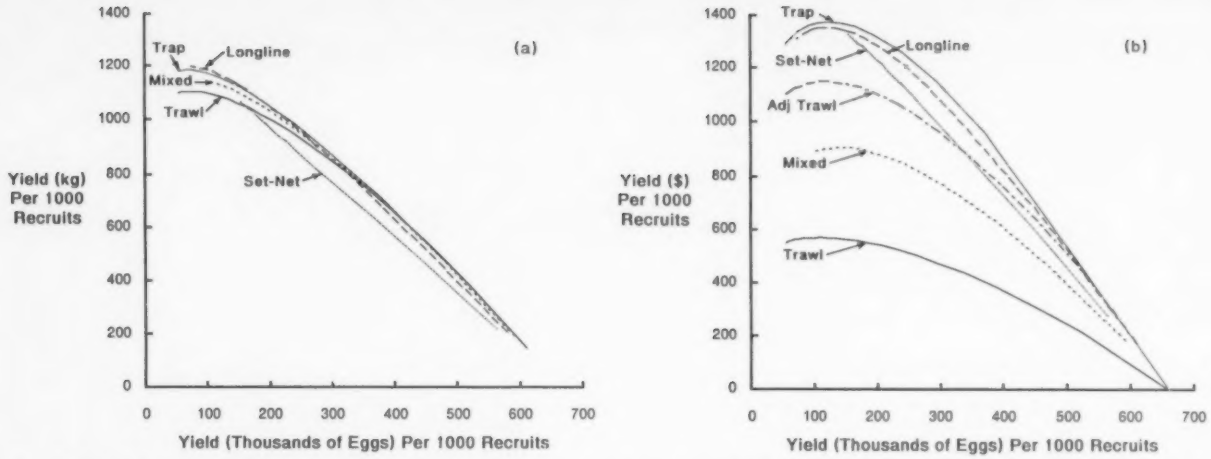

FIG. 6. Sablefish yields in (a) kg and (b) dollars per 1000 recruits as functions of egg yield per recruit for six methods of harvest. The adjusted trawl method is trawl gear that receives longline prices. The mixed method simulates the 1988 fishery in which 56% of the harvest is taken by trawl gear and 44% is taken by fixed gear.

TABLE 2. Population and catch characteristics (when recruitment is constant at 1000 individuals and egg yield per recruit is fixed at 226 000 eggs) for the six sablefish harvesting methods illustrated in Fig. 6. The adjusted trawl method is trawl gear that receives longline prices. "Expl. pop." is the portion of the total population that has recruited to the fishing grounds. "Expl Rate" is the biomass yield divided by exploitable biomass.

	No harvest	Trawl	Adjusted trawl	Trap	Longline	Set-net	Mixed gear
Yields							
Numbers	—	480	480	418	370	266	436
Biomass (kg)	—	968	968	1010	1003	921	995
Dollars	—	529	1078	1285	1248	1173	865
Catch stats							
kg/fish	—	2.02	2.02	2.42	2.71	3.47	2.28
$/kg	—	0.547	1.115	1.271	1.244	1.273	0.870
Total pop. stats							
Biomass (kg)	25 216	10 033	10 033	10 971	11 866	13 942	10 725
kg/fish	2.54	1.93	1.93	1.88	1.88	1.90	1.90
Expl. pop. stats							
Biomass (kg)	24 063	8927	8927	9833	10 725	12 789	9602
kg/fish	2.82	2.32	2.32	2.21	2.18	2.15	2.25
Expl. rate	—	0.108	0.108	0.103	0.094	0.072	0.104
Spawning pop.							
Biomass (kg)	13 084	4454	4454	4407	4373	4326	4405

(Fig. 8). The underlying dynamics responsible for this result can be illustrated by plotting yield and eggs per recruit for each gear type as functions of fishing effort (Fig. 9). When the age at 50% maturity is increased from 5 to 12 yr, the yield per recruit curves do not change, but the eggs per recruit curves shift downward because fewer eggs are produced. Since the decrease in egg production is greater for the longline strategy, it has lower yield than the trawl strategy for fixed levels of eggs per recruit.

The Arcto-Norwegian cod and sablefish examples illustrate that an examination of the relationship between the critical age and age at 50% maturity combined with the theoretical results from Getz (1979) and Reed (1980) will provide considerable insight into the type of age-specific harvesting strategy that will maximize yield. Species that have a critical age that is significantly lower than the age at 50% sexual maturity are likely to have optimal methods of harvest that involve only a harvest at some terminal age. These examples also illustrate the importance of estimating the selectivities of the competing fishing gears.

An important limitation for the general application of the methodology presented here is the possibility that the yield per recruit curves for different methods of harvest (represented as functions of egg yield per recruit) will cross. For example, in Fig. 6b the curves for the adjusted trawl and set-net methods of harvest intersect when the egg yield per recruit value is about 300 000. In such cases, each method of harvest would be superior over a certain range of egg yield per recruit values, and thus, it would be impossible to determine which method of

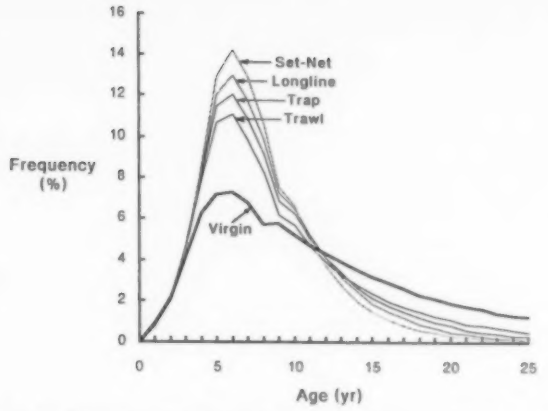

FIG. 7. Estimated age structure of the female spawning stock (when egg yield per recruit is fixed at 226 000) for an unfished ("virgin") sablefish population and for sablefish populations fished by four different methods of harvest: trawl, trap, longline, and set-net. As the fishing gear becomes more selective for larger fish (e.g. set-net gear), the age structure of the spawning stock becomes more concentrated around the younger age classes.

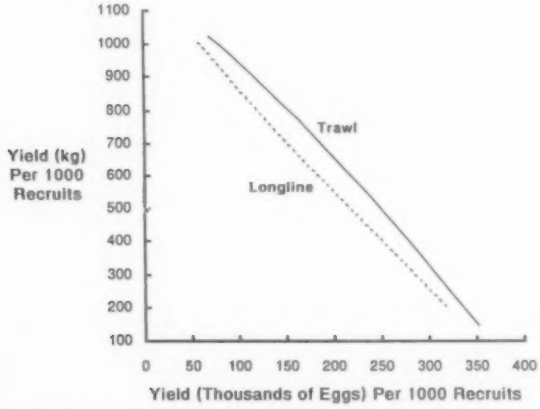

FIG. 8. Sablefish yields (kg) per recruit for trawl and longline gears when the age at 50% sexual maturity is increased from 5 to 12 yr. The age at which a cohort reaches maximum biomass (6.9 yr) is unaffected by this change. With this single change in life history parameters, the trawl method of harvest produces a biomass yield that is about 15% higher than that produced by the longline method of harvest. This contrasts with the case where age at 50% maturity is 5 yr, in which the longline method of harvest gave a slightly higher biomass yield (Fig. 6a). Thus, the relationship between critical age and age at 50% sexual maturity is important in determining what method of harvest produces the highest yield per recruit.

harvest produces the highest equilibrium yield without some knowledge of the spawner–recruit function.

A further limitation of this approach is that it assumes that all life history parameters remain fixed, regardless of the exploitation rate and population size. That is, it does not allow for compensatory mechanisms. Other researchers (e.g. Gunderson 1977; Jensen 1981; Ware 1985) have investigated the possible mechanisms by which an exploited population can maintain a constant egg production per recruit as fishing effort increases. Their general idea is that individuals within an

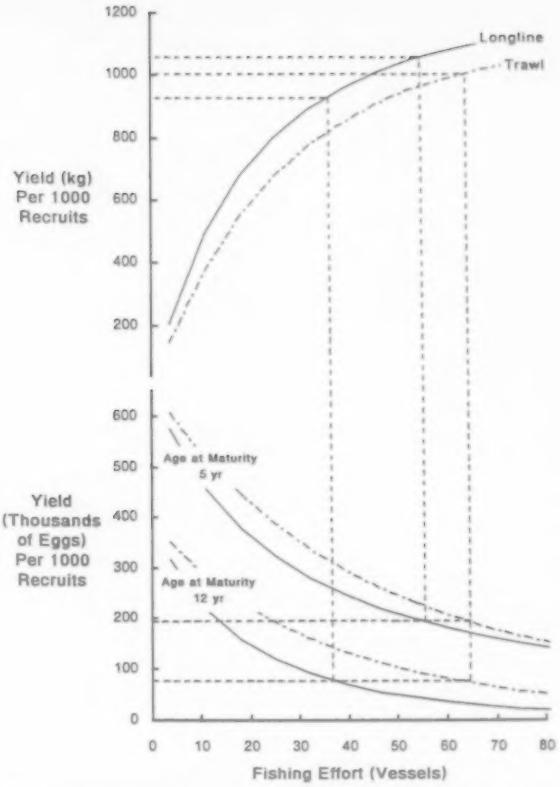

FIG. 9. Yields (kg and eggs) per 1000 recruits as functions of fishing effort for trawl and longline gears when the age at 50% maturity is 5 and 12 yr. Yield per recruit values are not affected by the parameter change whereas eggs per recruit declines as age at 50% maturity is increased. The decline is greater when the fish are harvested by longline gear, thus explaining the lower longline yields shown in Fig. 8.

exploited stock may grow faster (due to less competition), age at 50% sexual maturity may decrease (if maturity is determined by size rather than age), and as a result the reproductive value of each recruit may remain constant even though total mortality is increased. Gunderson (1977) concluded that, for Pacific ocean perch (*Sebastes alutus*), the required compensatory changes would have to be unrealistically large. However, Jensen (1981) concluded that, for lake whitefish (*Coregonus clupeaformis*), such compensatory changes were possible.

It seems unlikely that the presence of compensatory mechanisms would alter the relative yields from different methods of harvest, unless those methods of harvest resulted in different compensatory effects. When estimating the instantaneous rate of natural mortality (M) for the dynamic pool model, I found that different values of M did not result in different relative dollar yields from competing methods of harvest. I suspect that my approach is equally robust to minor changes in other life history parameters, such as the growth rate.

The methodology presented here requires some knowledge of the egg production process (fecundity or maturity functions) in addition to knowledge of the fishing mortality, survival, and growth processes. Most research programs for commercially important species provide estimates of at least the maturity function. The most difficult functions to estimate for this method will most likely be the selectivity functions for the dif-

ferent gear types. Since these functions are critical to this analysis, every attempt should be made to describe the selectivity functions as realistically as possible. Assuming knife-edged recruitment at age t_c for all gear types is unrealistic.

I suspect that a great many other fisheries have problems similar to the ones described here, and the methodology introduced in this paper may have broad application to a wide variety of allocation and by-catch problems. Two specific examples from Alaskan fisheries are (1) the roe versus surimi versus fillet fishery for walleye pollock (*Theragra chalcogramma*) and (2) estimating the lost yield to the longline fleet caused by the by-catch of juvenile Pacific halibut (*Hippoglossus stenolepis*) in the trawl fisheries for other species. Each of these problems is, in essence, a "method of harvest" problem in which managers wish to include reproductive considerations, but for which the spawner–recruit function is not well described.

Acknowledgments

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RETROSPECTIVE/RÉTROSPECTIF

A Brief Review of the International Council for the Exploration of the Sea (ICES) on the Occasion of the Formation of the North Pacific Marine Science Organization

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Elements of the first 90 years of the North Atlantic organization the International Council for the Exploration of the Sea (ICES) have been examined to illustrate its functions and some of its achievements. The 17-nation Council, founded in 1902 to deal with overfishing in northern European marine areas, now represents countries on both sides of the Atlantic. Its mandate is to promote marine science and provide advice on the rational use of marine living resources. To accomplish this it stimulates and coordinates cooperative research programmes in the biology of marine, anadromous, and catadromous species, mariculture, fisheries assessment, pollution, and physical and chemical oceanography.

L'auteur examine certains faits survenus au cours des 90 premières années du Conseil international pour l'exploration de la mer (CIEM), un organisme dont l'aire d'intérêt est l'Atlantique Nord, afin d'illustrer ses fonctions et certaines de ses réalisations. Le Conseil, que a été fondé en 1902 dans le but de lutter contre la surpêche dans les mers de l'Europe du Nord, regroupe maintenant 17 États répartis des deux cotés de l'Atlantique. Il a pour mandat de promouvoir les sciences de la mer et de fournir des conseils relatifs à l'utilisation rationnelle des ressources marines vivantes. Pour ce faire, il favorise et coordonne des programmes de recherche coopératifs en biologie des espèces marines, anadromes et catadromes, en mariculture, en évaluation des pêches, en étude de la pollution et en océanographie physique et chimique.

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The general belief that a North Pacific international organization devoted to the marine sciences would be valuable received impetus when informal discussions of the concept were held in Vancouver in 1973. Further meetings, informal and formal, culminated in a 1986 gathering at Anchorage where participants from Canada, the Peoples Republic of China, Japan, the Union of Soviet Socialist Republics, and the United States of America endorsed the concept of establishing an organization to promote and coordinate marine scientific investigations in the North Pacific Ocean (north of 30°N) and its adjacent seas and facilitate the exchange of scientific information; it was recommended further that the organization not have responsibility for allocation of marine resources. The consensus and opinions expressed at Anchorage indicated that the need for such an organization was widely recognized in the scientific community and that it was time to refer the concept to the five governments. Canada was asked to take the lead in drafting a concept paper. The draft articles were discussed in 1988 in Sidney, British Columbia (B.C.), and refined at a working group meeting in Seattle in 1989. The Draft Convention for a North Pacific Marine Science Organization was considered in Ottawa in 1990 and approved as an adequate instrument by representatives of the five countries who recommended it to their respective governments for signature and ratification. Ratification by at least three of the five countries is required to bring the convention into force; this was expected to occur by the fall of 1991 at which point other interested nations would be invited to participate. The organization was expected to be operational by late 1991 with its headquarters in Canada, at the Institute of Ocean Sciences, Sidney, B.C. This new body is the Pacific counterpart of the 17-member International Council for the Exploration of the Sea (ICES), the oldest intergovernmental organization dealing with marine sciences (its current membership is listed in the appendix). Since ICES was a partial model for the new organization and has been discharging its responsibilities for the North Atlantic for almost a century, it was considered appropriate to mark the inauguration of the North Pacific Marine Science Organization by presenting a brief review of salient features of the history of ICES.

ICES: The Beginning

Two quotations from Went's (1972) history of ICES succinctly describe the scene which led directly to its formation:

> In the middle of the last century there was a firm belief in the inexhaustibility of the seas. So great were the resources of the seas, many people believed that with his existing methods of capture, MAN could hardly make any impression on them. However, with the great expansion in the trawling fleet and the introduction of steam propulsion and the otter trawl, many thinking scientists had other views. In fact, some were satisfied that overfishing was taking place.
>
> Organized fisheries research as such was unknown but individual scientists were working on many marine problems. These men were, however, scattered, often isolated, with little contact with their fellow scientists. This is not surprising since communications were slow and there was little money for science and scientists.
>
> By the "nineties" of the last century, scientific investigations into many marine problems were being conducted in the Atlantic, the North Sea, and the Baltic. But scientists were beginning to realize that isolated investigations in limited areas of the sea were really of little value and that cooperation in the international field was highly desirable.

There had been a degree of cooperation in certain areas of fisheries, largely in their regulation and reduction of conflicting interests; witness the signing of the North Sea Convention of 1882. This, however, was insufficient and an initiative was taken by the British National Sea Fisheries Protection Association to organize a conference to consider the state of the fisheries in the North Sea. This conference, held in London in 1892, was attended by representatives from nations around the North Sea (Belgium, Denmark, France, Germany, The Netherlands, and the United Kingdom). Apparently, it was not a success, since it was described by a senior German representative, Walther Herwig, as characterized by "strong sentiment but little basic knowledge" (Went 1972). Herwig returned from the meeting convinced of the need for cooperative international research into the biology of the important fish species.

Since a number of leading marine scientists from northern European coastal states held similar views, a course developed which led more or less directly to the formation of ICES. Two organizing and founding conferences, one in Stockholm in 1899 and the other in Kristiania (now named Oslo) in 1901, determined the form and function of ICES. These were followed by the inaugural meeting, which began July 22, 1902, in Copenhagen, and was attended by representatives of Denmark, Finland, Germany, The Netherlands, Norway, Sweden, Russia, and the United Kingdom; Herwig was elected the first President. Over the years, membership in the Council has varied in keeping with events and changing circumstances. For example, the United States of America first adhered July 22, 1912, but did not return to the Council following the dislocation in Council affairs imposed by the First World War. Canada's interest in joining was sounded by the Council as early as 1912, but Canada did not join until 1967; the United States of America rejoined in 1973.

In the earlier organizational meetings, a program for oceanographic (or hydrographic work as it was then termed) and biological work had been planned. The policy statement which preceded the recommendations for this program, quoted in full by Went (1972), is included here as well, since it has proved to contain the guiding principles for the Council and is characteristic of the practical approach adopted by the Council from its very beginning:

> Considering that a rational exploitation of the sea should rest as far as possible on scientific enquiry, and considering that international cooperation is the best way of arriving at satisfactory results in this direction, especially if in the execution of the investigations, it be left constantly in view that their primary object is to promote and improve the fisheries through international agreements, this International Conference resolved to recommend to the States concerned the following scheme of investigations which should be carried out for a period of at least five years.

The initial program, although precisely planned, was far larger than could be carried out immediately with the resources available. Thus, a degree of selection was necessary. To aid in making choices aimed at furthering the purposes for which ICES had been formed, Johan Hjort of Norway, one of the prime movers, suggested that effort should be focused on a few problems of greatest practical importance. These were (Went 1972) "The migrations of herring and cod and the influence of these migrations on fisheries in the northern part of the North Sea and also the biology of these and other allied fishes, and the question of overfishing, particularly in the southern part of the North Sea, and in connection with this the special study of flat fish." To initiate and carry this program forward, three committees were formed: A. Committee on Migration of Food Fishes, B. Committee on Overfishing, and C. Committee for the Baltic.

Arrangements were also made for hydrographic (oceanographic) programs which were to be integral and important dimensions of all work. The Central Laboratory (1902–08) was set up in Kristiania (Oslo) under Fridtjof Nansen for the purpose of testing and improving instruments and methods and setting standards for physical and chemical measurements. Thus, the general approach to obtaining international collaboration in the marine sciences with emphasis on results of practical importance to fisheries was set. This approach, with suitable additions and variations, has been followed with success by ICES over the years. With the exception of the brief, but successful 6-year experiment with the Central Laboratory, it has not been considered necessary for the Council to operate its own experimental facilities. The activities of the Central Laboratory, which filled an important gap at the time, have been met since by national laboratories working alone or in conjunction with one another. The topics chosen, migration of food fishes (which, initially, was believed to be the cause of interannual variability in landings), concern for flatfish, especially plaice, and the influence of hydrographic (oceanographic) factors, would remain central to the Council's activities.

In this regard, it is interesting to read the analysis of the Council's early history prepared by Sinclair et al. (1987) as a background for a study to define the needs of fisheries for physical oceanographic information within the Canadian Atlantic Zone. This analysis placed considerable emphasis on the hydrographic (oceanographic) interest of various of the early ICES scientists (Nansen, Ekman, Pettersson, Hjort, among others) and especially the statement by Sverdrup (1955) that ICES ". . . was founded primarily for the purpose of applying oceanographic research to fisheries problems. . . ." Although this is probably something of an overstatement, the interest in oceanographic studies was high and was heightened by the fact that the Kristiania founding conference (1901) recommended that each member state should provide a steamer specially constructed for scientific fisheries research. This resolution was accepted and resulted in the building of a number of fisheries

research vessels in different countries. Given the high cost and the crucial importance of specialized vessels dedicated to marine research, this has to be considered as one of the Council's major achievements and one which made possible the establishment of fisheries research as a serious activity.

Sinclair et al. (1987) also drew attention to the fact that in the early days of the Council's history, the specific links between research in physical oceanography and fisheries questions were not obvious. Generally, it was considered that increases in the understanding of the physical characteristics of the ocean, including circulation and mixing, would be relevant not only to physical oceanography, but to fisheries as well. Part of the problem which existed then, and to a considerable extent still exists, has been reemphasized by Sinclair et al. (1987) as ". . . the inability given the respective states of art in oceanography and fisheries biology to define joint tractable questions." Incidentally, the study by Sinclair et al. was a determined and largely successful attempt to offset the past failures in this direction by providing for the Canadian Atlantic region, at least, clear identification of questions which could be tackled jointly. This is not to suggest that in the early days of ICES there was no progress, but rather that the oceanographic studies carried out by the member countries were not focused on specific fisheries questions. Progress came because the oceanographers, plankton specialists, and fisheries biologists frequently shared laboratories and vessels as well as participating in the same committees and, thus, were familiar with each others' concerns.

It is significant to note that ICES was formed in response to the need to deal with fisheries problems believed to be caused by overfishing. In its approach, it chose to concentrate on developing a comprehensive understanding of the behaviour, needs, and biology of food fishes in relation to oceanographic influences. Other choices could have been made in response to the same perception and, in fact, one other major course (stock enhancement) was pursued in parallel in the late nineteenth and the first half of the twentieth centuries. In that period, fisheries biologists of the United States, Great Britain, and Norway, in particular, released billions of larval marine fish, annually, in attempts to maintain or increase fisheries resources.

According to Shelbourne (1964), the marine fish hatchery and stocking programs appealed to governments because, he felt, they are inherently reluctant to impose controls to curb overexploitation. The underlying principle of the enhancement programs was the belief that the annual broodstock strength was a direct linear result of the number of eggs released by the adult fish. To compensate for the depletion of eggs through heavy fishing of spawning aggregations, the salvaged spawn was protected in hatcheries through the embryonic stages and the fry released to capitalize on food supplies believed made surplus through overfishing. The first commercial marine fish hatchery was built in the United States, at Woods Hole, and was complemented by two others in New England at Boothbay Harbor, Maine, and Gloucester, Massachusetts. The Norwegians had hatcheries at Flodevigen and Trondheimsfiord; the British established hatcheries at Dunbar, Aberdeen, Fleetwood, and Port Erin on the Isle of Man. These massive efforts were concentrated mainly on the Gadidae (cod, pollock, and haddock) and the Pleuronectidae (flounder, plaice, and sole) and released many millions of each of these species into the Atlantic Ocean and adjoining seas each year. According to Nash (1977) and Shelbourne (1964), by World War II or shortly after, the lack of evidence of positive results led to the termination of virtually all of these attempts to expand the marine food fish resources. Interestingly, Canada's extensive hatchery system for producing lobster larvae for release to bolster Atlantic coast lobster populations was terminated in 1917 for approximately the same reasons of high cost and lack of apparent results. Subsequent analyses suggest that these efforts had little likelihood of success, since the finfish and lobster larvae were released without much regard for their biology or food sources. These attempts, however, were not a total loss, since the marine fish hatcheries had become focal points for marine biologists to conduct in-depth studies of the various species. Some of the finfish hatcheries subsequently became famous marine research laboratories of today.

The Development of Modern Fisheries Research Concepts

Hjort was instrumental in bringing problems into better perspective and defining the issues so that cooperation amongst all groups would be more fruitful. In1913 and 1914 he undertook, through a set of lectures, to reiterate the proposition, formulated earlier, that the paramount need was for an explanation of the causes of the marked interannual variability in the quantity and quality of landings at given locations in northern Europe. The interannual variability was shown to result from year-class variability of geographically persistent age-structured populations. Although as Sinclair et al. (1987) stated, this interpretation is accepted as a fundamental concept today, it was reached only after a decade of systematic international research by fisheries biologists. The examples used by Hjort were herring and cod. Unfortunately, the herring aging technique using the scales became the subject of prolonged and acrimonious debate between Hjort and United Kingdom scientists led by D'Arcy Thompson. This debate continued for some 10 years and was considered by some to have been a major setback to fisheries research, since considerable additional effort had to be expended by the Norwegians to prove the validity of the scale aging technique in order to demonstrate clearly the age structure of the herring populations (Went 1972).

Notwithstanding the debate, the hypothesis shifted attention to discrete populations rather than focusing on the species alone and to Hjort's further contention that variability in landings resulted from fluctuations of abundance in individual year-classes, the relative abundance of which, he believed, was determined in the early life history stages. Two hypotheses followed from this: Critical Period Concept (e.g. food limitation for larvae) and Variable Role of Currents in advecting the early life history stages away from the appropriate distributional area for the population. To test these hypotheses, in particular the Critical Period Hypothesis, plans were drawn for joint studies to be carried out by the hydrographers, plankton specialists, and fisheries biologists. These ambitious plans, unfortunately, were overtaken by the outbreak of World War I. Attempts in 1938, again led by Hjort, to institute rather similar joint studies were again overtaken by war and the topic languished until 1951. In the meantime, the main thrust in physical oceanography was the investigation of the large-scale mean circulation of the deep ocean with limited emphasis on the variability in the continental shelf processes, thereby effectively removing the oceanographers from the fisheries scene and diverting their attention full-time to another major issue.

Modern Times: 1951 to Present

A special scientific meeting on Fisheries Hydrography, held in Amsterdam in 1951, came to the conclusion that a combination of biological, hydrographical (oceanographic), meteorological, physiological, and statistical researches had furthered knowledge of biological productivity, the habits of the fish stocks, and also the fisheries themselves. As a result, it recommended that a close association of disciplines be maintained and recommended a lengthy set of activities relating to oceanography and planktonology including definitions of problems the other committees wished the hydrographers (oceanographers) to attack. Sinclair et al. (1987) concluded that although much had been done, the goal of linking hydrography and fisheries, for which overall thrusts were taken by Hjort and his colleagues in ICES initially and advanced by Sverdrup, had not been realized fully. The two disciplines, oceanography and fisheries research, still intermingle in ICES and, thus, the opportunities and the needs still exist; the task remains to define the key questions jointly in terms on which both can agree and to work jointly toward a common objective.

In the main, ICES has provided the international forum for work in marine sciences aimed at providing a solid underpinning for North Atlantic fisheries. Since there were few people and resources to support marine science, and the problems usually transcended national areas, a system for international collaboration was the most efficient way to make progress. The Council did not operate by dictating courses of action, but rather, through consideration and discussion of the assembled data, attempted to define the issues more and more closely. Once it received concurrence that the choices were right, it then provided machinery to organize international assaults on these through joint experiments, working groups, a revised and comprehensive committee structure, special meetings, symposia, and its various publications. In 1959, the working groups became of major importance; since then they have proliferated to cover every topic of interest to ICES member countries. Much, if not most, of the intersessional work is carried by the flexible system of working groups composed of experts from all countries, working under the direction of one or more of the standing scientific committees, concentrating on topics from development of methods for measuring fish and shellfish populations, blooms of algae harmful to fish and shellfish stocks, mariculture, disease, and genetics to marine pollution and applied assessment groups preparing the formal advice to be reviewed by and passed through the two advisory committees for action by the responsible intergovernmental bodies such as the Northeast Atlantic Fisheries Commission, the International Baltic Sea Fisheries Commission, the North Atlantic Salmon Conservation Organization, the Convention for the Prevention of Marine Pollution by Dumping from Ships and Aircraft (Oslo Commission), the Convention for the Prevention of Marine Pollution from Land Based Sources (Paris Commission), and the Convention for the Protection of the Marine Environment of the Baltic Sea Area (Helsinki Commission). In 1990, for example, ICES conducted most of its work through the annual Statutory Meeting of the Council (the 78th), the two advisory committees (the Advisory Committee on Fishery Management (ACFM) and the Advisory Committee on Marine Pollution (ACMP)), 12 standing scientific committees (listed in the appendix), and 83 working, study, or planning groups plus seven workshops and two symposia held during the year. The work of the North Atlantic Salmon Working Group is typical.

An Example of Working Group Activities: The North Atlantic Salmon Working Group

Because of the increased catches of Atlantic salmon at west Greenland, in particular the spectacularly large catch in 1964, the International Commission for the Northwest Atlantic Fisheries (ICNAF) joined with ICES to organize a scientific appraisal of this fishery (Horsted 1988). The resultant ICES/ICNAF Joint Working Party on North Atlantic Salmon representing North Atlantic countries with Atlantic salmon interests began in 1966 its work which continued through the 1970s (Parrish and Horsted 1980). After ICNAF was succeeded by the Northwest Atlantic Fisheries Organization (NAFO) in 1979, this Joint Working Party was continued as the ICES Working Group on North Atlantic Salmon and under this new title held its first meeting also in 1979 (Horsted 1988). Tag recoveries had shown that salmon caught at Greenland originated in rivers and hatcheries of ICES member states from both sides of the Atlantic and not in Greenland rivers. Thus, ICES was a natural scientific forum in which to continue the discussions of the impact of the Greenland fishery on returns to home waters. In later years, the work expanded to include analyses of other salmon fisheries and, since 1984, to develop responses to scientific questions posed by the North Atlantic Salmon Conservation Organization (NASCO).

Driven by specific questions to ICES for practical advice, the Working Group brought together salmon biologists from both sides of the Atlantic to present and debate the results of their research. As in almost all working groups, consensus was achieved on precisely worded responses to potentially controversial questions. In addition, the meetings led to development and acceptance of assessment models and to the identification and international coordination of research projects for Atlantic salmon. As with other working groups, research recommendations were reviewed by the parent committee, in this case the Anadromous and Catadromous Fish Committee (ANACAT). In recent years, Working Group meetings have been seen, increasingly, as appropriate fora for presentation and review of biological research and now compete with the annual ANACAT meetings in this respect.

The North Atlantic Salmon Working Group, as with all stock assessment working groups, reports to the ACFM, which is the only body empowered by the Council to advise on fishery management questions. It is composed of a Chairman, one representative from each ICES member country, the Chairmen of the Demersal Fish Committee, the Pelagic Fish Committee, and the Baltic Fish Committee, and the ICES Statistician, together with an observer from the European Community (EC), and an observer for the Faeroe Islands and Greenland. Twice a year the ACFM reviews working group reports and formulates advice for the appropriate bodies; it also provides feedback to working groups on the methodology used, helping to achieve a consistent standard and approach across the many species and stocks considered.

Another example of the important and excellent work done by ICES working groups has been illustrated by Thurberg (1988) in an article on studies of biological effects of contaminants.

Special Meetings and Symposia

One device used by ICES to discuss emergent, controversial, or important issues is the series of Special Meetings or Sym-

posia which ICES sponsors, events which are two to four days in duration, often convened prior to an annual statutory meeting and are open to all interested in an in-depth treatment of the selected topic. Attempts are made to draw definite conclusions which will aid in guiding future work. These have been extremely successful in defining more closely the issues and are held at a time when it appears possible to clarify and crystallize perceptions or concepts which hitherto have been rather hazy or unorganized. A few chosen more or less at random indicate something of their scope:

(1) Conference on North Sea Plaice (1925)
(2) Second Special Meeting on Racial Investigations (1928)
(3) Special Meeting on the Fluctuations in the Abundance of the Various Year-classes of Food Fishes (1929)
(4) Special Meeting on Size Limits for Fish and Regulation of Meshes of Fishing Nets (1934)
(5a) Special Scientific Meeting on Fisheries Hydrography (1951)
(5b) Special Scientific Meeting on Overfishing (1951)
(6a) Problems and Methods of Sampling Fish Populations (1954)
(6b) Herring Tagging Techniques and Results (1954)
(6c) Oyster and Mussel Culture (1954)
(7) Symposium on North Sea Fish Stocks — Recent Changes and Their Causes (1975)
(8a) ICES/EIFAC Symposium on Eel Research and Management (1976)
(8b) Special Meeting on Population Assessments of Shellfish Stocks (1976)
(9) Symposium on the Assessment and Management of Pelagic Fish Stocks (1978)
(10) Special Meeting on Diseases of Commercially Important Marine Fish and Shellfish (1980)
(11) Symposium on North Sea Dynamics (oceanography) (the Council assisted in an organizational role) (1981)
(12a) Special Meeting on Causes, Dynamics and Effects of Exceptional Marine Blooms and Related Events (1984)
(12b) Symposium and Workshop on Contaminant Fluxes Through the Coastal Zone (1984)
(13) Symposium on Marine Sciences of the Arctic and Sub-Arctic Regions (1987)
(14a) Symposium on Early Life History of Fish (1988) (the third on this topic)
(14b) Symposium on Baltic Sea Fishery Resources (1988)
(15a) Symposium on the Ecology and Management Aspects of Extensive Mariculture (1989)
(15b) Symposium on Multispecies Models Relevant to Management of Living Resources (1989)
(16a) Symposium on Case Histories of the Effects of Introductions and Transfers on Aquatic Resources and Ecosystems (1990)
(16b) Symposium on Shellfish Life Histories and Shellfishery Models (1990).

When the special meetings, symposia, or projects are examined in detail, it is apparent that the Council's current activities are consistent with its origins and the foresight shown by its founders; a few accounts developed further illustrate this.

The Symposium on North Sea Fish Stocks — Recent Changes and Their Causes, held in 1975 (Hempel 1978), is a particularly good example, since questions about causes of changes in fish stocks in the North Sea were prime factors leading to the formation of ICES originally. This symposium focused on three main questions: what had happened to North Sea stocks and their environment in the past two decades, to what extent could those changes be explained, and what kind of data, experiments, and models would help to understand fluctuations and long-term trends. Briefly, the conclusions were as follows: catches had more than doubled since the 1960s; many changes in stocks were apparent, but the causes of the changes could not be ascribed with confidence; and biological background information was still insufficient for models of intra- and interspecific interactions (i.e. physiological regulation of growth, maturation, and reproduction; regulation of stock size by ecological factors such as cannibalism, competition for food and space, and thinning out by fishing; and the influence on these processes of physical or chemical variations in the environment). The recommendations specified, among others, the need for improved statistical information, studies on the question of replacement species, nutrient levels and larval food supplies, and increased international collaborative, multidisciplinary work among fishery biologists and "pure" biological and physical oceanographers.

Another excellent example is afforded by the Symposium on the assessment and Management of Pelagic Fish Stocks held in 1978 (Saville 1980). This too was a large meeting which attracted many of the scientists involved with pelagic fish. It was also timely, since many of the major pelagic stocks were overfished or had collapsed, i.e. Georges Bank herring, Atlanto-Scandian herring, North Sea herring, North Sea mackerel, Celtic Sea herring, California sardine, Peruvian anchoveta, and the Japanese sardine fishery to name some. Conclusions drawn were that pelagic stocks are more fragile than demersal fish stocks because of their behaviour (schooling) and the fact that they are usually characterized by large year-classes occurring at lengthy intervals with poor recruitment in between. In addition, there was evidence that as stock size decreased in pelagic fish, the catchability coefficient increased; thus, with modern communications and fish-finding aids, it was possible that reduced nominal effort could maintain or even increase exploitation rates on a reduced stock. In addition to the deficiencies in biological and ecological understanding of pelagic fish and their stocks, it was concluded that part of the reason for the collapse of the various stocks was that, commonly, abundance was overestimated and effort was underestimated. This resulted in a misunderstanding of the power of the fleet and its impact on schooling fish. Aiding and abetting the process were deficiencies in the scientific advice offered and a less than perfect resolve to apply effective management measures in time. Specific courses, following logically from these observed deficiencies, were recommended to improve the underlying science, scientific advice, and management mechanisms and action. Although many of the recommendations have been implemented, management improved, and positive results observed, one very clear lesson is that recovery of collapsed pelagic stocks, in particular, can be a long process.

In both of the symposia described above, as well as in other fora, it had become apparent that there were serious shortcomings in both biological knowledge and assessment methodologies. As a consequence, recognition of the limitations of the traditional single species assessments (i.e. it is not possible to vary only one element at a time) led in 1975 to a decision by the Council to initiate work to develop and test multispecies assessment models. Accordingly, the Ad Hoc Working Group on Multispecies Assessment Model Testing was formed and at its first meeting (1980) considered what information would be

needed to test appropriate models. They concluded that while in the past, assessment groups had chosen to assume that natural mortality was constant over the life span of the species and over large ranges of exploitation rates, it should be possible to improve on this assumption by means of new models incorporating species interactions. In the models proposed, the central feature was that natural mortality should not be a fixed input parameter, but, at least, partially modulated by inter- and intraspecific predation. Fishing mortality and natural mortality values were to be estimated simultaneously for each age group and year in a given catch array. The additional information required was a suitability index of each prey age group for each predator age group and the rate of total food consumption. Although this type of assessment was theoretically possible, application was hindered by a lack of knowledge of fish feeding habits and preferences. Thus the decision to concentrate on species interaction Virtual Population Analysis (VPA) models brought in its train the need to emphasize research on food consumption by major predators of commercially important fish species.

Accordingly, the Working Group recommended an intensive stomach-sampling scheme for cod, whiting, saithe, mackerel, and haddock from the North Sea. This recommendation was accepted by the Council and the "Stomach Sampling Project 1981" was undertaken with member countries making available extensive research vessel time and analytical capacity to carry out this extremely complex and expensive program, coordinated through ICES. Adjustments had to be made in the initial plan to produce adequate sampling intensities, and improved methods for recording and analyzing stomach contents; these then had to be related to ages, lengths, and weights. The handling of data and the many other aspects of a program as large and complex as this constituted major logistical challenges; it, of course, could not be completed in the single year but had to be extended past the mid-1980s to deal with the vast amounts of data. At its conclusion, the scientists involved in the Stomach Sampling Project stressed the need to repeat the exercise in some form, since there is a strong requirement to test the hypothesis that ecological vulnerability is constant from year to year and that although the project had shown considerably higher predation on harvested species than was formerly assumed, it is a narrow basis for completely revising general views of the level of predation mortalities.

Although improvements can be expected, the current methodology of multispecies assessments is considered by the Working Group as essentially complete, following absorption into the process of the results of the modified and extended Stomach Sampling Project. The Ad Hoc Working Group on Multispecies Assessments believes that although the Multi-Species Virtual Population Analysis (MSVPA) was specifically designed for the North Sea, it is potentially applicable for simultaneously assessing predation and fishing mortalities in a variety of situations in other areas such as the Baltic, Icelandic, or North American waters, thus once again offering compelling leadership to the whole fisheries research community on an extremely important issue. In addition, it is felt that this methodology should be used to provide *long-term advice* for the nine North Sea species included in the MSVPA, since this cannot be provided properly through single-species assessments. At this time, the consensus within ACFM is that although the preceding statement is largely correct, the methodology needs further development before it can be usefully applied.

Shellfish, Marine Pollution, and Mariculture

Although the stimuli which led to the formation of ICES initially were largely related to overfishing of finfish and the concomitant problems, it was recognized, at the time, that there were other problems and opportunities. Murawski (1988) in his review pointed out, "Even prior to the first meeting of ICES in 1902, European and North American researchers were pursuing shellfish related research along three relatively divergent paths: 1) mariculture (primarily of oysters and mussels, 2) effects of sewage and industrial pollutants on shellfish sanitation and abundance and 3) population dynamics and fishery regulation of natural stocks." In various guises, all of these are still very much a part of ICES activities. The shellfish research picture has been examined in depth by Murawski (1988) who in that context stated, "the challenge for the future is to conduct multidisciplinary studies aimed at understanding the impacts of management decisions regarding mariculture, pollution/contamination and harvesting of natural populations in the context of coastal ocean ecosystems. Current relationships among shellfish research programs within ICES will, by necessity, be modified to accommodate research of a more interdisciplinary nature."

Pollution, as noted above, was an early Council concern and at the meeting held in April 1912, plans were drawn concerning the effects of pollution on salmon and their spawning grounds (Pearce 1988). Pearce, in reviewing marine pollution work, mentioned that the question of oil pollution was raised as early as 1927 and that Odon de Buen of Spain was invited to prepare a paper on its ill effects on fish and fisheries. The concern with pollution persisted and increased through the years leading in 1966 to the formation of a new standing scientific committee, the Fisheries Improvement Committee. The responsibilities of this committee included, among other matters, pollution and mariculture. Within the next decade it became apparent that the increasing problems of pollution and the accelerating interests and opportunities in mariculture could no longer be accommodated within a single committee.

Accordingly, the bulk of the responsibilities of the Fisheries Improvement Committee were divided between two new committees, the Marine Environmental Quality Committee (MEQC) and the Mariculture Committee which met for the first time in 1978. The MEQC was concerned with "the scientific study of man-made impacts other than fishing on the sea and its living resources, in particular studies of pollution," a mandate which has required an extensive programme of work by the committee and its associated working groups as the problems caused by pollution continue to mount (Pearce 1988). The Mariculture Committee, to a large extent an enlargement and amplification of the by now disbanded Working Group on Mariculture, was charged with the review and coordination of "investigations relating to culture of marine organisms, including transplantation and introduction of new species."

Formation of the Mariculture Committee was a timely recognition of the significance of culture in the overall fisheries picture. At the turn of the century, as Murawski (1988) mentioned, mariculture was concerned largely with oyster and mussel culture to replace lost shellfish production. Since then, first through immense increases in molluscan shellfish production and then beginning in the 1970s, the burgeoning finfish production (mainly salmonids) made it apparent that mariculture was becoming a significant source of fishery products using methods quite different from traditional fisheries and also with

quite different needs, although much of the mariculture opportunities actually grew out of the "early life history studies" conducted earlier. Mariculture production in ICES countries now exceeds 0.5 million tonnes annually and in Norway, for instance, the cultured salmonid production is approximately equal in value to the traditional marine fisheries. The bulk of this activity takes place in the coastal zones where other fisheries, pollution, recreational activities, transportation, and many industrial activities are paramount. Thus the problems faced by mariculturists are not only those occasioned by intensive and extensive husbandry (nutritional, physiological, environmental, disease, genetics, seed, technological, etc.) but also stem from competition for space and the need to maintain or improve water conditions. Despite these constraints, mariculture is expanding substantially and appears to be on the verge of bringing into production other species such as cod, haddock, halibut, Arctic char, wolffish, and scallops. In all of this the ICES Mariculture Committee and its associated working groups have played an important and catalytic role.

International Cooperation

The Council, although first on the ground, is no longer alone. It has worked productively in the past and continues to do so with other organizations such as the International Commission for the Exploration of the Mediterranean Sea (ICEMS), ICNAF and its successor NAFO, the Intergovernmental Oceanographic Commission (IOC/UNESCO), the Scientific Committee on Ocean Research (SCOR/UNESCO), and the Food and Agriculture Organization of the United Nations (FAO) including certain subsidiary bodies such as the European Inland Fisheries Advisory Commission (EIFAC). Some of these have been heavily influenced in their composition and operations by the lead offered by ICES.

Those wishing a more detailed treatment of the structures and mechanisms that ICES has used over the years to accomplish its objectives are referred to the history of Went (1972) and to the succinct and comprehensive treatment of this topic by Pawlak (1988).

Summary

Today we believe that the conclusion drawn in the early years of the century was correct, that is the improvement (management) of fisheries should be attempted through the rational application of the results of scientific enquiries rather than by arbitrarily chosen empirical measures. Given the lengthy period required and the high cost of conducting scientific studies coupled with the always pressing or urgent need for solutions, the trick has been to select the key items or indices from a bewildering array of complex choices to determine how much information was enough, and to weave the results into practical measures which would permit rational exploitation of the sea, ie., "turning its resources to the best advantage in the present without prejudice to the future" (Went 1972) encapsulated in today's crisper, but somewhat less precise terminology "sustainable development" as enunciated in the Bruntland Commission Report (WCED 1987).

Any attempt to summarize the activities of ICES over the years and even to highlight its successes runs the risk of being a mere catalogue or of introducing distortion. A few statements, however, should be made. The Council, in its approaches, has not only initiated international collaboration in the marine sciences in direct response to the question of overfishing, but also laid the foundations which established fisheries research as a credible discipline. From the first, it has been successful in defining major issues and in providing the organizational machinery to mount relevant collaborative studies to acquire the scientific underpinning for rational management of the living resources of the sea. As a direct result of its cooperative approach aimed at practical results, it has been responsible for and influential in the provision by member countries of specialized ships for fisheries and oceanographic work, the institution of laboratories, and acquisition of staff trained in marine sciences. From the outset, it has specialized in breaking down generalized concerns such as overfishing into questions which can then be investigated in detail, e.g. migration and behaviour of food fishes which led rather directly to Hjort's hypotheses on age-structured populations and practical concepts and ways of getting at such issues as interannual variability. In the course of doing this, the influence of food plankton and other prey and oceanographic features (environmental influences on food and migration) became major parts of the Council's interests. All of these, of course, encompassed extremely practical and important studies on ways to age fish, standard methods to report data (age/length/weight), sampling of stomach contents to determine food choices and multispecies interactions, as well as major programs leading to commercial culture of fish and shellfish. Always there has been an insistence upon the goal of developing broad concepts which would improve the understanding of the living resources and the driving forces, as well as providing a forum for discussion of all fisheries research questions.

The Council recognized from the beginning that estimates of fish stocks and fishing efforts, to be soundly based, would require national statistical information collection systems. This element, crucial to assessment processes today, received early attention and encouragement over the years for nations to adopt compatible statistical systems and report fully on their commercial fisheries through ICES.

Understanding the life history of the various species has always been considered important by ICES as has the definition of stocks, the impact of various fishing gears on the fisheries, and ways to reduce their adverse effects. An illustration of the rudimentary state of knowledge of at least one species, the eel, at the time of the founding of ICES is provided by the report of Committee C (Baltic) in 1905. It stated that it was now convinced that eel did not spawn in freshwater or in the Baltic or Norwegian Sea. The early concern for marine mammals (seals as well as whales) resulted in a Whaling Committee, which predated the International Whaling Commission, and thus was the only body in a position to recommend international programs in 1927 on the major species for the purpose of conserving the stocks. The Council in 1929 and 1930 made a series of recommendations and drafted a convention on whaling responsibilities which was ultimately adopted by the International Whaling Commission. This is only one of the many instances where the work of the Council resulted in more formal arrangements to absorb and apply advice on fisheries and to guard against "overfishing," the underlying concern which originally brought ICES into existence.

In his opening address to the 68th Statutory Meeting of ICES, President Hempel (1980) offered this description: "ICES is a strange body with considerable diversity of structures and functions which can be summarized under two headings: a) Promotion of marine science, and b) Advice to governments on

the rational use of marine living resources and their protection against pollution." To achieve these functions cited by the President, ICES operates by stimulating and coordinating cooperative research programs in population biology and ecology of marine, anadromous, and catadromous species, mariculture, fisheries assessment, pollution studies, and physical and chemical oceanography relevant to the dynamics and productivity of marine resources. The results are reported in an ICES family of publications, the main ones being the *Journal of Marine Science* (formerly *Journal du Conseil*), the ICES *Marine Science Symposia* (previously *Rapports et Procès-Verbaux des Réunions*), the ICES *Cooperative Research Reports, Techniques in Marine Environmental Sciences*, and the ICES *Identification Leaflets*.

I hope that this brief discussion of ICES is useful to those engaged in organizing the North Pacific Marine Science Organization and that its first 90 years will be as successful and productive as the first 90 years have been for ICES.

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Appendix

Member Countries

Belgium, Canada, Denmark, Finland, France, Germany, Iceland, Ireland, The Netherlands, Norway, Poland, Portugal, Spain, Sweden, United Kingdom, United States of America, Union of Soviet Socialist Republics.

ICES Headquarters and Permanent Secretariat

Palaegade 2-4, 1261 Copenhagen K, Denmark.

Current Standing Scientific Committees

Anadromous and Catadromous Fish, Baltic Fish, Biological Oceanography, Demersal Fish, Fish Capture, Hydrography, Mariculture, Marine Environmental Quality, Marine Mammals, Pelagic Fish, Shellfish, Statistics.

Advisory Committees

Advisory Committee on Fishery Management, Advisory Committee on Marine Pollution.

LETTERS ET COMMENTS
LETTRES ET COMMENTAIRES

Phosphorus and Nitrogen Limitation of Phytoplankton Growth in Oligotrophic Lakes: Comment on McCauley et al. (1989)

It has proved difficult to make assessments of algal nutrient limitation in lakes based on bioassay enrichment studies (Dodds and Priscu 1990; Elser et al. 1990). Therefore, it was a valuable effort by McCauley et al. (1989) to collect a large data base on summer average chlorophyll (Chl *a*), total phosphorus (TP), and total nitrogen (TN) observations from 266 lakes and to fit a generalized linear model (sensus McCullagh and Nelder 1989) in both TP and TN to their data. Unfortunately, I think their conclusion regarding the relative role of TP and TN in limiting algal growth is an artifact of their method. They found that log TP, $(\log TP)^2$, $(\log TP)^3$, and the product (log TP)·(log TN) had highly significant partial effects on the logarithm of chlorophyll concentration. The curves log Chl $a = f$(log TP, log TN) are represented in a log Chl *a*/log TP graph by a family of sigmoid curves that converged at low phosphorus concentrations. This is in contrast with results by Smith (1982), who found a family of parallel lines. The authors claim that the convergence has two implications for lake management: at low concentrations of TP (<30 $mg \cdot m^{-3}$, e.g. in oligotrophic and mesotrophic lakes, OECD (1982) definitions of trophy) the chlorophyll concentration is little affected by TN; high concentrations of TP (>1000 $mg \cdot m^{-3}$) have little or no effect on chlorophyll concentrations. However, based on their equations, small changes in TN and TP of the same numerical value will give about the same change in Chl *a* concentration for oligotrophic lakes. Typical changes, ΔTP, between years in such lakes are 3–10 $mg \cdot m^{-3}$ (Seip et al. 1990). More important, fig. 2D in McCauley et al.'s paper, which also is the basis for their conclusion, shows a striking feature. The curve Chl $a = f$(TP) for TN = 5·TP shows that Chl *a* decreases with increasing TP

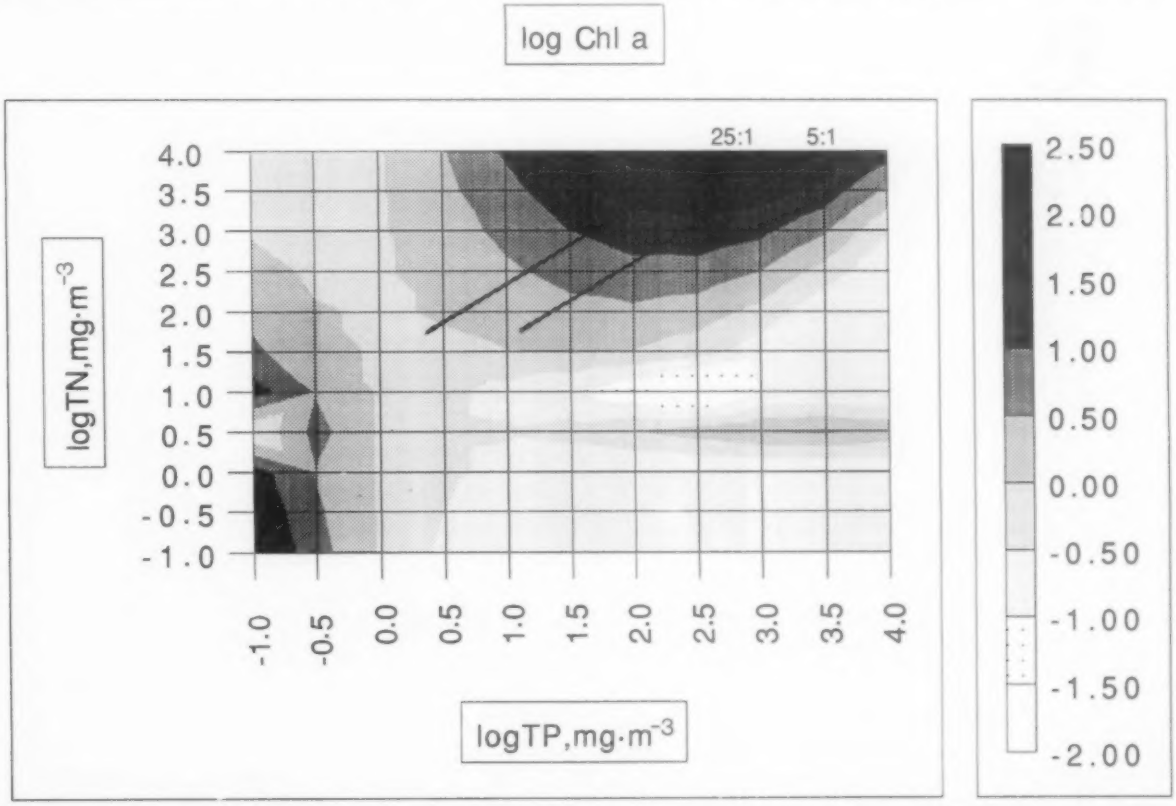

FIG. 1. Response surface showing summer epilimnetic Chl *a* concentration as a function of summer epilimnetic TP and TN concentrations in 266 lakes. The surface corresponds to the regression log Chl $a = -0.83 \log TP + 0.34 (\log TP)^2 - 0.12 (\log TP)^3 + 0.43 (\log TP) \cdot (\log TN) + 0.03$, $n = 875$, found by McCauley et al. (1989). Lines show TN:TP ratio equal to 5:1 and 25:1 (by mass). The lines end approximately at lowest observed value of TN. Lowest and highest observed values of TP are 1 and 14 095 $mg \cdot m^{-3}$ and of TN are 61 and 10 740 $mg \cdot m^{-3}$.

in the regions 1 $mg \cdot m^{-3} < TP < 3\ mg \cdot m^{-3}$ and $TP > 600\ mg \cdot m^{-3}$. Their calibration region for TP is 1–14 093 $mg \cdot m^{-3}$ and for TN is 61–10 740 $mg \cdot m^{-3}$.

To explore this feature further, I depicted the response surface for Chl *a* to changes in both TP and TN (Fig. 1) corresponding to McCauley et al.'s equation for the version "combined model" (literature data as source). The response surface underscores the nonsigmoid particularities of the curves shown by McCauley et al. Since the author's management advice with regard to TP and TN depends upon the characteristics of the log Chl $a = f$ (log TP, log TN) curves close to an apparently anomalous domain, one should probably either give a theoretical justification for the anomaly or examine if the anomalies are artifacts of the method. It is difficult to explain that for constant TN, chlorophyll may decrease with increasing TP (cf. Fig. 1 at low TN:TP ratios; the ratio between the largest TN and TP values in the data set is 0.8). However, contrary to logistic expressions, third-order polynomials have an upper and a lower maximum and thereby negative derivatives. Furthermore, since the independent variables TP and TN probably are partly colinear, the coefficients of the polynomial expression may be inflated (Reckhow et al. 1987). Thus, based on a visual assessment of the response surface in Fig. 1, and the arguments above, I feel that the analysis of McCauley et al. does not prove that "variation in TN concentration in oligotrophic systems has little, if any, consequence to algal biomass" — Knut L. Seip, *Senter for industriforskning (Center for Industrial Research), Forskningsvn 1, P.O. Box 124 Blindern, N-0134 Oslo 3, Norway.* (JB003)

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Different Effects of Phosphorus and Nitrogen on Chlorophyll Concentration in Oligotrophic and Eutrophic Lakes: Reply to Seip

Establishing the role(s) of the many nutrients that might affect the observed biomass and production of phytoplankton throughout the natural domain of lakes is a daunting task. Results from manipulation experiments along with evidence gathered from natural variation in levels of nutrients and chlorophyll provide key pieces of the puzzle. While Elser et al. (1990) synthesized and criticized experimental results on phosphorus (TP) and nitrogen (TN) limitation, McCauley et al. (1989) evaluated the relative role of the two nutrients by examining their empirical relationship with chlorophyll concentration among lakes throughout the Northern Hemisphere, thereby extending the initial work of Smith (1979). Seip has questioned one of the conclusions presented in McCauley et al. regarding the asymmetrical effect of phosphorus and nitrogen in lakes of different trophic status. McCauley et al. concluded that the effect of these nutrients varies depending on the level of phosphorus in the lake. This conclusion was drawn from two sets of analyses: (1) a model-free inspection of the data showing that the phosphorus–chlorophyll relationship is sigmoidal (a result independently established by Prairie et al. (1989)) and (2) a multivariate regression analysis of the influence of nitrogen and phosphorus on chlorophyll levels throughout a broad collection of lakes. Based on the parametric regression analysis, McCauley et al. found that "the effect of nitrogen is much greater at high TP concentration than at low" and that "the phosphorus–chlorophyll relationship is a family of sigmoid curves that converge at low phosphorus concentration." These conclusions differ considerably from the original interpretation

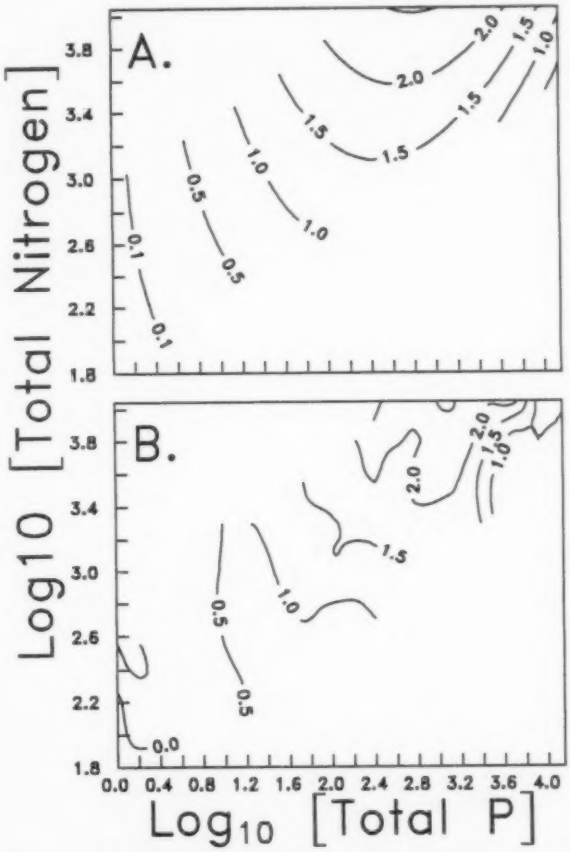

FIG. 1. (A) Predicted $\log_{10}$ chlorophyll concentrations from McCauley et al.'s combined model, where predictions were made only within the range of TP, TN, and chlorophyll *a* observed in world lakes (cf. Seip's fig. 1). (B) Contours of observed $\log_{10}$ chlorophyll concentrations in world lakes determined using an inverse squared distance technique followed by cubic-spline smoothing. All concentrations are $\mu g \cdot L^{-1}$.

of Smith (1979) that the relationships consist of a parallel series of lines.

Seip questions only the validity of the interpretation of the parametric model presented by McCauley et al. for oligotrophic lakes and suggests that we failed to replicate Smith's family of parallel relationships between TP and chlorophyll due to the particular quadratic model that we chose. We disagree with Seip that our original interpretation is incorrect, and we support our original conclusion in two ways: (1) by showing that the asymmetrical effect of nitrogen and phosphorus is present in the contour plot presented by Seip based on our parametric model and (2) by examining the raw data themselves without model fitting to provide evidence that our findings result from the data and not from our choice of statistics.

Before proceeding, however, it is important to recognize that the predictions of the regression model must be examined only over the range of the independent variables. Clearly, models can often predict spurious (and often ludicrous) results if applied outside the range of data from which they were derived. Therefore in the analyses presented below, we restrict the contour plots to the realistic range of log TP and log TN values.

Figure 1A shows the contour plot of predictions of chlorophyll concentration from our combined model when limited to the range of natural variation of log TN and log TP. Once the contour plot is restricted to the range of data present in the original analysis, the asymmetrical effect of phosphorus and nitrogen on chlorophyll is readily apparent from the asymmetry in the isoclines at both low and high phosphorus levels. A nearly identical response to nitrogen and phosphorus is seen in a simple contour plot of the *data* (Fig. 1B). To illustrate this asymmetry at low phosphorus levels, consider an oligotrophic lake with log TP (micrograms per litre) = 0.5. Lakes with this level of phosphorus have an average of 308 $\mu g\ TN \cdot L^{-1}$ or log TN = 2.48 as determined from our original dataset. If you locate this point on the log TN – log TP surface (Fig. 1) and then ask what effect does a unit change in log TP or log TN have on the estimate of chlorophyll *a*, you observe that the change in log TP predicts an increase in chlorophyll response from the 0–0.5 range to the 0.5–1.0 range whereas a unit change in log TN still predicts chlorophyll levels *within* the original range of 0–0.5. In both Fig. 1A and 1B, isoclines of chlorophyll *a* concentration are nearly vertical at low phosphorus concentrations, but nearly horizontal at high phosphorus concentrations. Chlorophyll concentration therefore appears to vary little with TN in oligotrophic lakes but varies greatly with TN in eutrophic lakes. Chlorophyll concentrations are very sensitive to variation in phosphorus concentration in oligotrophic lakes, and insensitive to variation in phosphorus concentration in eutrophic lakes. These predictions are consistent with the conclusions presented in McCauley et al. and are independent of statistical fitting methods.

The polynomial equation presented in McCauley et al. are one of many models that could describe the same result. No matter what model is chosen, the result is the same: TP concentration is correlated differently with chlorophyll at different combinations of phosphorus and nitrogen. Chlorophyll concentration covaries primarily with TP in oligotrophic lakes and primarily with TN in eutrophic lakes — Edward McCauley, *Ecology Division, Department of Biological Sciences, University of Calgary, Calgary Alta. T2N 1N4, Canada*, and John Downing, *Département de Sciences Biologiques, Université de Montréal, Montréal, Québec H3C 3J7, Canada.* (JB105)

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ANNOUNCEMENTS/AVIS

International Society for Diatom Research
and
Nederlands-Vlaamse Kring van Diatomisten

12th International Diatom Symposium

30 August to 5 September 1992

Renesse (Zeeland)
The Netherlands

Programme

The programme will cover the whole field of diatom research. Contributions will be expected to span a broad range of subjects including:

1. Marine and freshwater ecology
2. Palaeoecology
3. Stratigraphy
4. Taxonomy and morphology
5. Water quality and pollution.

The Organizing Committee wishes to put special emphasis on the effects of anthropogenic activities on the environment. Therefore, papers on subjects such as monitoring, eutrophication, acidification, ecotoxicology, and so on are especially welcome.

Papers can be submitted for publication in the proceedings to be published after the symposium.

Venue

"De Zeeuwse Stromen" is a luxurious hotel and conference centre, situated in the southwestern part of the Netherlands (Zeeland), just outside the little town Renesse.

Renesse is situated on Schouwen-Duiveland, one of the Zeeland isles, approximately 45 minutes from Rotterdam and 2 hours from Amsterdam, Antwerp, and Brussels by car. Arrangements will be made to transport participants of the symposium from Rotterdam Railway Station which has a direct and fast train connection with Schiphol (Amsterdam) International Airport.

Registration, Costs, and Further Information

The tentative fee for attending the 12th International Diatom Symposium will be Dfl 300 for members of the International Society for Diatom Research and Dfl 400 for nonmembers.

The Organizing Committee has negotiated very favourable terms for your stay in "De Zeeuwse Stromen." Estimated costs for the 6-day symposium are Dfl 900. This includes coffee, tea, lunches, and meals.

All further details about the programme, accommodation, and mid- and postconference tours are available from the Conference Secretariat, 12th International Diatom Symposium, AquaSense, P.O. Box 41125, 1009 EC Amsterdam, The Netherlands. Telephone: (31) 20 5922244; Fax: (31) 20 5922249.

International Society for Diatom Research
et
Vlaamse Kring van Diatomisten (Pays-Bas)

Douzième symposium international sur les diatomées

du 30 août au 5 septembre 1992

Renesse (Zélande)
Pays-Bas

Programme

Le programme couvre tout le domaine des recherches sur les diatomées. Les communications devraient porter sur une large gamme de sujets, notamment :

1. Écologie marine et dulcicole
2. Paléoécologie
3. Stratigraphie
4. Taxonomie et morphologie
5. Qualité de l'eau et pollution.

Le comité organisateur souhaite mettre l'accent sur les effets environnementaux des activités anthropiques. Les communications traitant de sujets tels le monitorage, l'eutrophisation, l'acidification, l'écotoxicologie, etc., sont donc particulièrement recherchées.

Des communications peuvent être soumises pour publication dans le compte rendu du symposium.

Lieu

Le « De Zeeuwse Stromen » est un hôtel et un centre de conférences luxueux situé dans le sud-ouest des Pays-Bas (Zélande) à proximité de la petite ville de Renesse.

Renesse est située sur l'île Schouwen-Duiveland, une des îles de la Zélande, à environ 45 minutes par la route de Rotterdam et 2 heures d'Amsterdam, d'Anvers ou de Bruxelles. Des dispositions seront prises pour le transport des participants à partir de la gare de Rotterdam qui est elle-même reliée par train rapide à l'aéroport international de Schiphol (Amsterdam).

Frais d'inscription et renseignements divers

Les frais d'inscription au symposium ont été temporairement à 300 florins pour les membres de la « International Society for Diatom Research » et à 400 florins pour les non membres.

Le comité organisateur a négocié des coûts d'hébergement très favorables au « De Zeeuwse Stromen ». Les coûts du séjour de 6 jours, qui comprennent les repas, etc., ont été estimés à 900 florins.

Des précisions sur le programme, l'hébergement et les visites faites pendant ou après la conférence peuvent être obtenues en s'adressant au Secrétariat des conférences, 12e symposium international sur les diatomées, AquaSense, C.P. 41125, 1009 EC Amsterdam, Pays-Bas. Téléphone: (31) 20 5922244; Télécopieur : (31) 20 5922249.

Symposium on Freshwater Mussel Conservation and Management

October 11–14, 1992

The Symposium will be held at the Embassy Suites Hotel, St. Louis, MO. Sessions will be devoted to regulations, commercial harvest, conservation, sampling methodology, data management, and environmental awareness. Further information: Kurt Welke, Wisconsin Department of Natural Resources, 111 W. Dunn St., Prairie du Chien, WI 53821, USA. Telephone: (608) 326-0233.

Symposium on Freshwater Mussel Conservation and Management

du 11 au 14 octobre 1992

Le symposium aura lieu au Embassy Suites Hotel, St. Louis, MO. Les sessions seront consacrées aux règlements, à la récolte commerciale, à la conservation, aux méthodes d'échantillonnage, à la gestion des données et à la prise de conscience vis-à-vis de l'environnement. Renseignements : Kurt Welke, Wisconsin Department of Natural Resources, 111 W. Dunn St., Prairie du Chien, WI 53821, USA. Téléphone : (608) 326-0233.

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